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ANNALS OF THE
SOUTH AFRICAN MUSEUM

ANNALE VAN DIE
SUID-AFRIKAANSE MUSEUM

VOLUME 96

BAND 96

ANNALS OF THE SOUTH AFRICAN MUSEUM
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VOLUME 96 BAND

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THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

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CAPE TOWN

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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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A NEW SPECIES OF *SEPIA* (CEPHALOPODA, SEPIIDAE) FROM SOUTH AFRICA

By

MARTINA A. ROELEVELD

&

W. R. LILTVED

Cape Town Kaapstad

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MARTINA A. ROELEVELD

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W. R. LILTVED

South African Museum, Cape Town

(With 14 figures and 4 tables)

[*Ms accepted 31 July 1984*]

ABSTRACT

A new species of the genus *Sepia* is described from the Atlantic Coast of the Cape Peninsula, South Africa. *Sepia pulchra* sp. nov. is the fifth species of *Sepia* maturing at a small size (MLd approx. 20 mm) to be recorded from South African waters. The female animal most closely resembles *S. dubia*, which has been placed in the problematic subgenus *Hemisepius*. However, the shell of *S. pulchra* indicates that this species is more closely related to members of the subgenus *Sepia* s.s. The use of the ventral keels on the mantle, and the position of spermatophores on the hectocotylus, are illustrated for the first time in sepiids.

CONTENTS

INTRODUCTION

On a series of SCUBA dives off the Atlantic Coast of the Cape Peninsula a number of small sepiids were collected by one of us (W.R.L.). These specimens were originally thought to be *Sepia dubia*, a species known from a single female specimen (Adam & Rees 1966: 119–120), also from South Africa.

On closer examination the newly acquired specimens were found to differ from the description of *S. dubia* in the sucker arrangement on the ventral arms and the structure of the shell. A re-examination of the holotype of *S. dubia*

Ann. S. Afr. Mus. **96** (1), 1985: 1–18, 14 figs, 4 tables.

showed that the female animals of both *S. dubia* and the new specimens do not seem to differ significantly (the male of *S. dubia* being unknown). The shells, however, are quite different.

The measurements, indices and abbreviations used in this paper are defined by Roeleveld (1972: 196). Additional measurements and counts are as follows:

EMLv —effective ventral mantle length, i.e. excluding that part of the mantle lying outside the limits of the ventral keels; measured along the ventral midline from the anterior edge of the mantle to the posterior limit of the keels.

HcL —length of the hectocotylized (left ventral) arm.

MHL —length of the (proximal) modified portion of the hectocotylus, from the most proximal suckers to the first normal (distal) suckers; the length of the modified portion is calculated as a percentage of the total length of the hectocotolized arm (HcL) and not of the mantle length.

Club suckers—the total number of suckers on the tentacular club.

Furthermore, an estimate of the maturity stage of each specimen is indicated by a roman numeral I–III (see Table 1). Since the sex, size and maturity

TABLE 1

Definition of maturity stages.

Maturity stage	*Male*	*Female*
I: immature	Spermatophores absent; testis small, undeveloped.	Ovary and nidamental glands small, undeveloped.
II: maturing	Testis and accessory reproductive glands partially developed, but spermatophores absent.	Ovary and nidamental glands partially developed; no eggs visible in ovary.
III: mature	Spermatophores present in Needham's sac, penis and/or on hectocotylus.	Nidamental glands large; fully developed eggs present in ovary.

stage affect the morphology (especially the degree of modification of the hectocotylus in males), these conditions are relevant in comparing specimens. A particular specimen can then conveniently be designated, for example, ♂ III 24, indicating a mature male with a dorsal mantle length of 24 mm.

Sepia pulchra sp. nov.

Figs 1–14; Tables 2–4

Material

Holotype: SAM–S1036, ♂ III 17, Llandudno, Cape Peninsula, 25 m, collected by W. R. Liltved, 11 October 1982, SCUBA; deposited in the South African Museum.

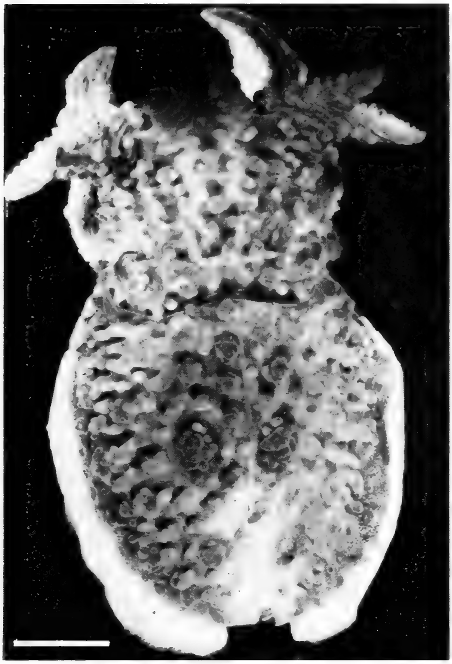

Fig. 1. *Sepia pulchra* sp. nov. Dorsal view of holotype, SAM–S1036, ♂ III 17. Scale = 5 mm.

Paratypes: SAM–S822, ♂ III 22, Hottentots Huisie, Cape Peninsula, 15 m. SAM–S982, ♀ III 21, Bakoven, Cape Peninsula, 21 m. SAM–S1007, ♂ III 16, ♀ II 17, Llandudno, Cape Peninsula, 25 m (same data as holotype). SAM–S1029, ♂ III 19, ♀ II 21, Llandudno, Cape Peninsula, 26 m. SAM–S1030, ♀ III 22, Llandudno, Cape Peninsula, 40 m. SAM–S1031, ♂ III 17, ♂ III 18, Llandudno, Cape Peninsula, 30 m. SAM–S1032, ♂ III 19, ♀ III 22, Llandudno, Cape Peninsula, 30 m. SAM–S1033, ♂ III 20, ♀ III 24, Llandudno, Cape Peninsula, approx. 50 m. SAM–S1034, ♂ III 15, Hottentots Huisie, Cape Peninsula, 15 m. SAM–S1038, ♀ III approx. 19, Llandudno, Cape Peninsula, 32 m. SAM–S1039, ♀ III 19, Llandudno, Cape Peninsula, 35 m.

Diagnosis

Mantle with numerous complex dorsal papillae and fleshy ventral keels; suckers biserial on arms I–III and distally on arms IV, quadriserial proximally on arms IV; sexual dimorphism involving sucker enlargement on arms II and sometimes III and modification of sucker shape and size on right arm IV in males; tentacular club with subequal suckers; shell not calcified, delicate, broadly oval, with phragmocone extending to anterior margin, with reflexed inner cone and no posterior spine.

TABLE 2

Sepia pulchra sp. nov. Indices and counts for males.

	SAM–S822 ♂ III 22	SAM–S1033 ♂ III 20	SAM–S1029 ♂ III 19	SAM–S1032 ♂ III 19	SAM–S1031 ♂ III 18	*Holotype* SAM–S1036 ♂ III 17	SAM–S1031 ♂ III 17	SAM–S1007 ♂ III 16	SAM–S1034 ♂ III 15	*n* 9	*Mean*	*Range* MLd 15–22 mm
MLv	90,9	95,0	105,3	89,5	94,4	100,0	94,1	93,8	100,0	9	95,9	89,5–105,3
EMLv	72,7	80,0	94,7	73,7	77,8	82,4	82,4	81,3	86,7	9	81,3	72,7–94,7
MW	77,3	60,0	73,7	73,7	72,2	76,5	82,4	81,3	73,3	9	74,5	60,0–82,4
HL	40,9	55,0	63,2	63,2	55,6	58,8	58,8	62,5	60,0	9	57,6	40,9–63,2
HW	59,1	55,0	68,4	63,2	61,1	64,7	58,8	62,5	66,7	9	62,2	55,0–68,4
FL	100,0	95,0	89,5	94,7	100,0	100,0	105,9	100,0	93,3	9	97,6	89,5–105,9
FW	22,7	20,0	26,3	21,1	22,2	23,5	29,4	25,0	26,7	9	24,1	20,0–29,4
AL I	40,9	45,0	47,4	52,6	44,4	52,9	52,9	43,8	46,7	9	47,4	40,9–52,9
II	45,5	50,0	47,4	47,4	50,0	58,8	58,8	56,3	53,3	9	51,9	45,5–58,8
III	50,0	50,0	57,9	57,9	55,6	58,8	58,8	56,3	53,3	9	55,4	50,0–58,8
IV R	59,1	55,0	57,9	57,9	66,7	70,6	64,7	62,5	60,0	9	61,6	55,0–70,6
HcL	54,5	50,0	52,6	57,9	61,1	58,8	58,8	62,5	60,0	9	57,4	50,0–62,5
MHL (% HcL)	58,3	60,0	60,0	45,5	54,5	70,0	60,0	60,0	55,6	9	58,2	45,5–70,0
TL R	81,8	125,0	142,1	89,5	55,6	105,9	100,0	125,0	120,0			
L	77,3	135,0	105,3	94,7	88,9	100,0	82,4	150,0	173,3			
Tcl	13,6	15,0	26,3	21,1	16,7	—	17,6	25,0	20,0	8	19,4	13,6–26,3
Club suckers	60	57	57	60	59	59	60	68	—	8		57–68

Description

The animals are small, attaining maturity at a dorsal mantle length of 15–22 mm in males and 19–24 mm in females.

The mantle is broadly oval, its anterior margin convex dorsally and deeply emarginate ventrally around the funnel. The fins are of variable width, usually fairly wide, beginning relatively far back (the distance between the anterior ends of the mantle and fin is 23–33% MLd). Posteriorly the fins are rounded and separate.

The colour is reddish-brown dorsally on the mantle, head and arms, with the pigmentation of the mantle extending on to the bases of the fins. Mid-dorsally on the mantle there is a large oval purplish patch. The entire dorsal surface of the mantle, head and arms is covered with tubercles of variable size and complexity. The tubercles occur as three main types: simple tubercles, complex turrets, and even more complex flat oval tubercles. The larger tubercles are arranged in a distinct pattern that can be traced in all the specimens, although not all the tubercles of the pattern are readily distinguishable in every specimen. The degree of distinction of these large tubercles depends on the preservation and degree of skin contraction or 'wartiness' of the specimen; in addition, a particular large tubercle may have an overall flat oval appearance in one specimen and be more turret-like in another.

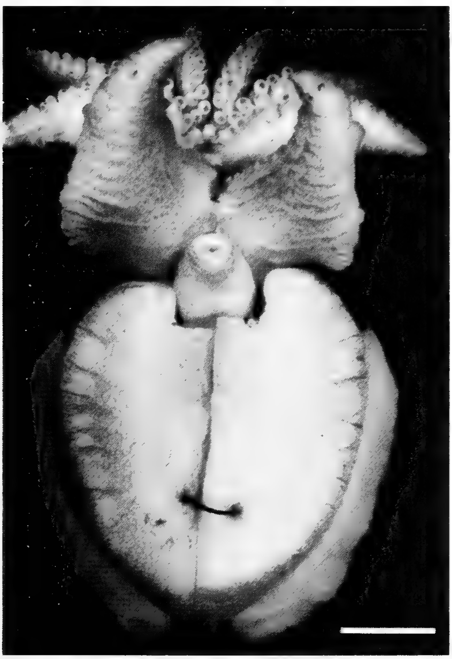

Fig. 2. *Sepia pulchra* sp. nov. Ventral view of holotype, SAM–S1036, ♂ III 17. Scale = 5 mm.

TABLE 3

Sepia pulchra sp. nov. Indices and counts for females.

	SAM–S1033 ♀ III 24	SAM–S1032 ♀ III 22	SAM–S1030 ♀ III 22	SAM–S1029 ♀ II 21	SAM–S982 ♀ III 21	SAM–S1039 ♀ III 19	SAM–S1007 ♀ II 17	*n* 7	*Mean*	*Range* MLd 17–24 mm
MLv	100,0	100,0	100,0	104,8	100,0	100,0	94,1	7	99,8	94,1–104,8
EMLv	79,2	86,4	90,9	90,5	71,4	89,5	88,2	7	85,2	71,4–90,9
MW	70,8	72,7	72,7	76,2	76,2	84,2	88,2	7	77,3	70,8–88,2
HL	58,3	63,6	68,2	57,1	52,4	57,9	76,5	7	62,0	52,4–76,5
HW	50,0	59,1	59,1	66,7	57,1	57,9	64,7	7	59,2	50,0–66,7
FL	87,5	100,0	90,9	95,2	104,8	105,3	105,9	7	98,5	87,5–105,9
FW	25,0	18,2	22,7	23,8	28,6	26,3	23,5	7	24,0	18,2–28,6
AL I	37,5	40,9	36,4	42,9	38,1	42,1	47,1	7	40,7	36,4–47,1
II	41,7	40,9	40,9	42,9	42,9	47,4	52,9	7	44,2	40,9–52,9
III	45,8	45,5	40,9	52,4	47,6	52,6	58,8	7	49,1	40,9–58,8
IV	50,0	54,5	50,0	52,4	52,4	57,9	58,8	7	53,7	50,0–58,8
TL R	162,5	118,2	145,5	157,1	128,6	115,8	141,2			
L	166,7	127,3	136,4	171,4	157,1	100,0	200,0			
Tcl	20,8	22,7	18,2	23,8	23,8	21,1	23,5	7	22,0	18,2–23,8
Club suckers	63	66	56	—	61	61	62	6		56–66

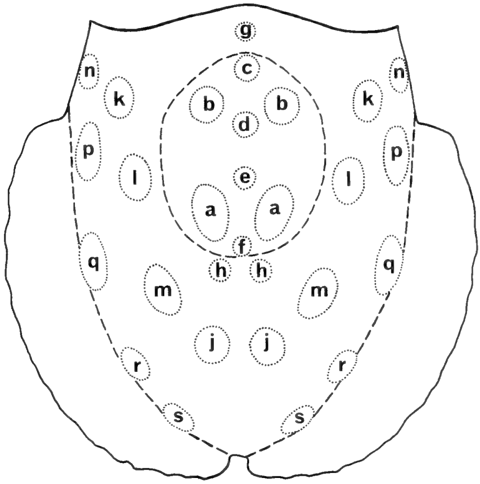

Fig. 3. *Sepia pulchra* sp. nov. Diagrammatic representation of relative sizes and distribution of the larger tubercles on the dorsal mantle surface.

In most specimens (including the holotype) three larger tubercles form cirri over each eye. On the mantle the pattern is most readily traced from the dorsal median patch. The patch bears two large, flat, oval tubercles (Fig. 3, a) posteriorly and two turrets (Fig. 3, b) anteriorly; four slightly smaller turrets (Fig. 3, c–f) run along the midline of the patch. The first of these median turrets (Fig. 3, c) is sometimes enlarged, forming a group of three with the two lateral turrets (Fig. 3, b). The median line of turrets on the patch is continued anteriorly by a single turret (Fig. 3, g) between the patch and the anterior mantle margin. Immediately posterior to the patch a pair of turrets (Fig. 3, h) straddles the dorsal midline; a second and somewhat larger pair of turrets (Fig. 3, j) occurs halfway between the posterior end of the patch and the posterior mantle margin. The latter pair of turrets (Fig. 3, j) is part of a series of eight tubercles (Fig. 3, j–m) that are arranged around the patch in a line roughly parallel to the lateral and posterior margins of the mantle. The six anterior tubercles of this lateral line are usually flat oval tubercles, whereas the posteriormost pair (Fig. 3, j) is turret-like. A marginal line of tubercles (Fig. 3, n–s) lies outside the lateral line. The first two tubercles (Fig. 3, n) of the marginal line lie anterior to the fins and the remaining tubercles are on the fin bases, alternating in position with the tubercles of the lateral line. The marginal line usually consists of ten flat oval tubercles. The spaces between the primary tubercles are filled with smaller tubercles ranging from simple to fairly complex, with several protrusions. All the principal tubercles described above are present in the holotype, but the posteriormost four tubercles (Fig. 3, r–s) of the marginal line are not very clearly distinguishable.

The ventral surface of the mantle, head and arms IV is buff in colour and forms a sole, made up of a pair of fleshy keels on the mantle and the swollen under-surfaces of the ventral arms (Fig. 2). The keels do not extend to the posterior end of the mantle, nor to the fin bases laterally; the lateral and posterior areas between the keels and fin bases are a somewhat lighter shade of the colour of the dorsal mantle surface.

The arms are short and stout, with well-developed fleshy protective membranes. The upper three pairs of arms are joined by an interbrachial membrane. Arms I and II are trapezoid in cross-section, with a flattened aboral surface; arms III and particularly arms IV bear lateral keels.

The suckers are globose, with small apertures. The sucker rings have a smooth inner edge, without teeth.

In the females, the suckers are biserial on arms I, II and III, though when the arms are compressed the suckers may give the appearance of being triserially or even quadriserially arranged on the proximal half of the arm, this compression most commonly occurring on the lateral arms (II and III). The suckers are largest near the base of the arm and gradually decrease in size distally. On the ventral arms of the females the suckers are quadriserially arranged on the proximal half to two-thirds of the arm but become biserial on the distal part.

In males the left ventral arm is hectocotylized. The proximal two-thirds of the arm is modified: the oral arm surface is wider than usual and bears numerous transverse folds. The suckers of the modified portion are reduced in size and form two longitudinal series of suckers on either side of the ridged oral region. The dorsal suckers clearly pertain to two longitudinal series as the suckers alternate in a zigzag manner. The two ventral series of suckers have merged to form an almost straight longitudinal row. Distal to the modified portion, the suckers are biserial.

In the holotype, the hectocotylus bears two pairs of widely separated suckers proximally. The dorsal and ventral margins of the modified region each bear eleven alternating lateral and medial suckers. Distally the arm bears seven to eight pairs of biserial suckers; the first few pairs of biserial suckers are larger than those in the modified region, but the sucker size decreases towards the arm tip. In the other males the number of suckers bordering the modified portion of the hectocotylus varies from ten to fourteen on either side of the ridged region.

The right ventral arm is also modified in males. Proximally there is a group (usually eight) of large globose suckers, irregularly arranged. Following these there are two to four medium suckers and two to four minute suckers; these occur either as a transverse row of four medium-sized suckers followed by two minute suckers, one on each extreme edge of the oral surface, as in the holotype, or as one medium-sized sucker on each extreme edge of the oral arm surface followed by minute suckers in a transverse row of four. This proximal group of suckers, which occupies about 40 per cent of the arm length, is followed by a pair of highly modified suckers (usually the 15th and 16th from the arm base). These suckers (Fig. 5) are greatly enlarged and asymmetrically

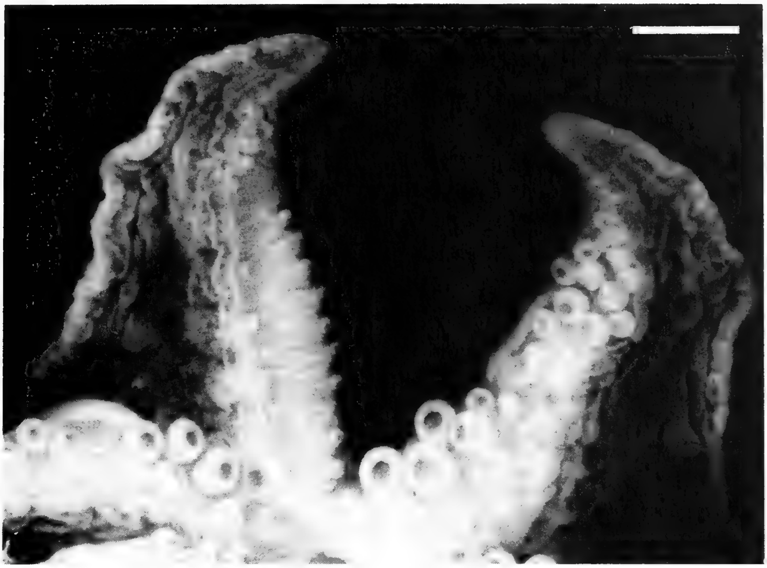

Fig. 4. *Sepia pulchra* sp. nov. Hectocotylus and right ventral arm of holotype, SAM–S1036, ♂ III 17. Scale = 2 mm.

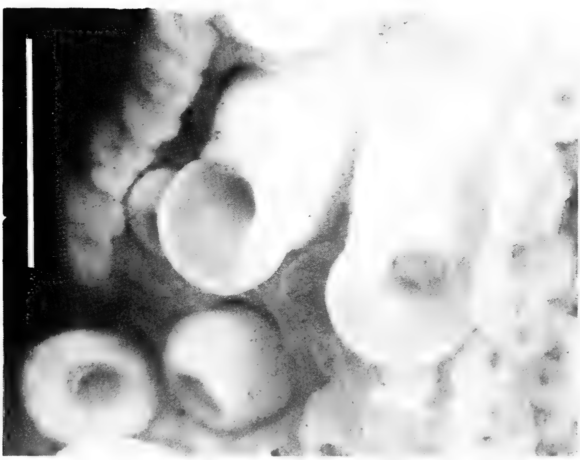

Fig. 5. *Sepia pulchra* sp. nov. Detail of modified suckers on right ventral arm of holotype, SAM–S1036, ♂ III 17. Scale = 1 mm.

elongate, with the ring proximal to the main body of the sucker, their overall shape being reminiscent of the pitcher plant (*Nepenthes*). The modified suckers are followed by a pair of very small suckers. In contrast, the next pair (usually the 19th to 20th suckers) is much larger, attaining at least the size of the medium suckers of the proximal group. Thereafter 24 to 28 suckers gradually reduce in size to the arm tip and are generally biserially arranged, though contraction of the arm may sometimes give a quadriserial appearance to the suckers on the middle of the arm. In one specimen (SAM–S1007, ♂ III 16) a second pair of suckers (the 19th to 20th) is modified as well as the 15th to 16th suckers on the right ventral arm, though not to the extent of the more proximal pair.

A further form of sexual dimorphism is shown in the enlargement of several suckers towards the tips of the lateral arms in males. The most marked sucker enlargement occurs on arms II, where there are usually three (but occasionally four) pairs of enlarged suckers in the 8th to 12th pairs from the arm base. A tendency towards enlargement of suckers is sometimes also shown on arms III. Where present, this enlargement affects one to three (usually two) pairs of suckers in the 10th to 14th rows from the arm base. In the holotype there are seven enlarged suckers on each arm II; these suckers pertain to the 8th to 11th pairs on left II and the 9th to 12th pairs on right II. There is no marked enlargement of suckers on arms III in the holotype.

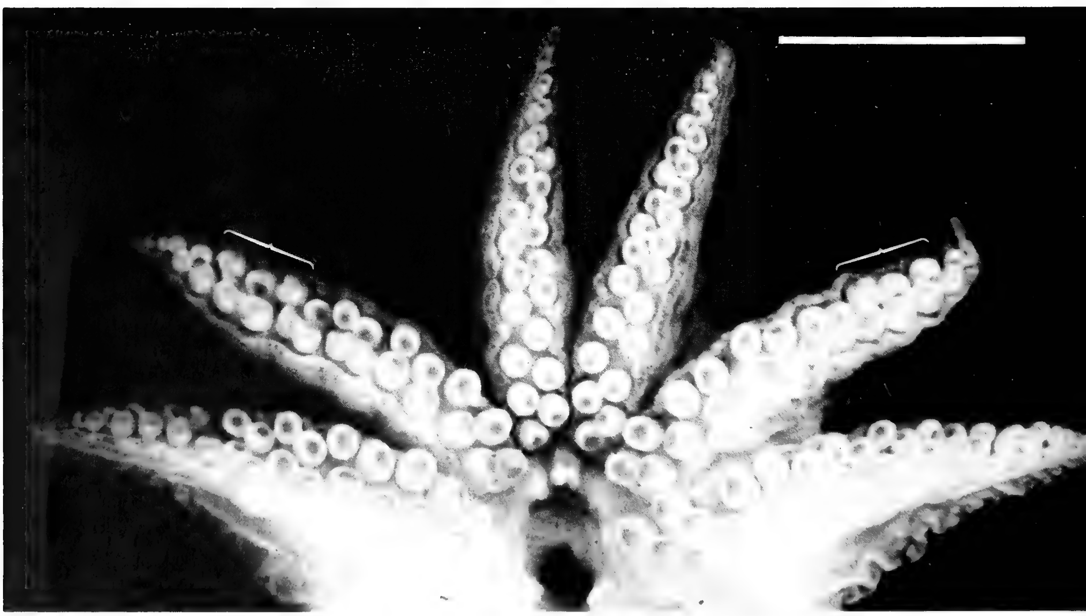

Fig. 6. *Sepia pulchra* sp. nov. Dorsal and lateral arms of holotype, SAM–S1036, ♂ III 17, showing enlargement of distal suckers on arms II (brackets). Scale = 5 mm.

The tentacular club is short and broad, somewhat recurved, and bears subequal suckers in transverse rows of four to six. The dorsal protective membrane is well developed and separate proximally from the ventral protective membrane, which curves around the base of the club. The natatory membrane is broad and continues along the tentacular stalk beyond the proximal end of the club. A terminal pad found on the club of many *Sepia* species, e.g. *Sepia faurei* (Roeleveld 1972, fig. 16b) and *S. robsoni* (Adam & Rees 1966, pl. 46, fig. 279), is situated at the anterior end of the dorsal protective membrane and is of similar size and shape to the club suckers. The dorsal surface of the club bears several transverse rows and a number of scattered chromatophores.

The beaks, radula and spermatophore are illustrated in Figures 8 and 9. The lower beak of SAM–S1033, ♀ III 24, has the following dimensions (after Clarke 1962 and Wolff 1982): rostral length (RL) 0,86 mm, wing length (WL) 3,24 mm, rostral tip to inner margin of wing (RW) 4,08 mm, crest length (CL) 3,26 mm, hood length 1,50 mm, jaw-angle width (JW) 1,66 mm. The hood and lateral wall are darkened around the rostrum and jaw angle, but leave a clear strip between them along the jaw edge. The darkening of the lateral wall gradually diminishes posteriorly and the wing is only slightly pigmented. The jaw angle is indistinct and obtuse, and is not obscured by a wing fold. The lateral wall has no distinct ridge or fold and there is no indentation in its posterior margin. The wing is long in relation to the rostrum (WL/RL 3,8).

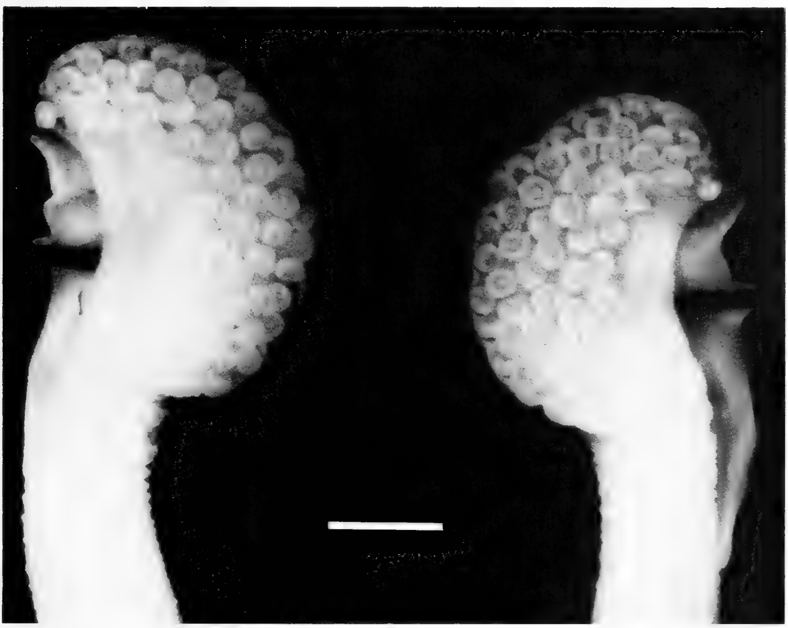

Fig. 7. *Sepia pulchra* sp. nov. Tentacular clubs, SAM–S822, ♂ III 22. Scale = 1 mm.

TABLE 4

Sepia pulchra sp. nov. Indices for shells.

	SAM–S822 ♂ III 22	SAM–S982 ♀ III 21	SAM–S1038 ♀ III *c.* 19	SAM–S1039 ♀ III 19	*Holotype* SAM–S1036 ♂ III 17	*n*	*Mean*	*Range*
L in mm	21	19	19	*c.* 19	16	5		16–21
W	52,4	63,2	63,2	*c.* 57,9	56,3	5	*c.* 58,6	52,4–63,2
Str z	*c.* 71,4	*c.* 57,9	63,2	*c.* 52,6	62,5	5	*c.* 61,5	*c.* 52,6–*c.* 71,4

The shell is not calcified and is broadly oval, becoming somewhat angular anteriorly; posteriorly the shell is broad, with a strong ventral curvature and a dorsal hump over the posterior end of the phragmocone. There is no posterior spine. The dorsal surface of the shell is finely reticulate and shows no distinct median ridge; the striae of the phragmocone are clearly visible through the thin dorsal shield. The phragmocone covers virtually the entire length of the shell and is very thin; the ventral surface is flat or somewhat concave, with at most an indistinct median groove; the striated zone is long and triangular, the striae wavy with an overall convex shape. The inner cone is reflexed and fused to the outer cone; in the holotype it is narrow, the limbs of the inner cone extending anteriorly along the lateral edges of the striated zone; in a larger shell (SAM–S1038, Fig. 9A) the inner cone is rather broader laterally, then tapers rapidly and twists, curving over the lateral edge of the striated zone. The outer cone is very broad laterally but narrow posteriorly, separating the posterior end of the inner cone from the shell edge by a narrow strip of outer cone.

Remarks

The female animals of *Sepia pulchra* are difficult to distinguish from *S. dubia*. Adam & Rees (1966: 120) described the arm suckers of *S. dubia* as being biserial, but re-examination of the holotype, ♀ II 17, showed that, as in

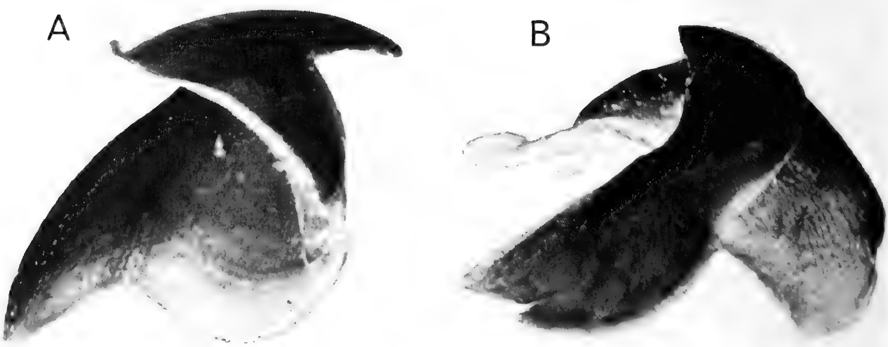

Fig. 8. *Sepia pulchra* sp. nov. Beaks, SAM–S1033, ♀ III 24. A. Upper beak, rostral length 1,0 mm. B. Lower beak, rostral length 0,86 mm.

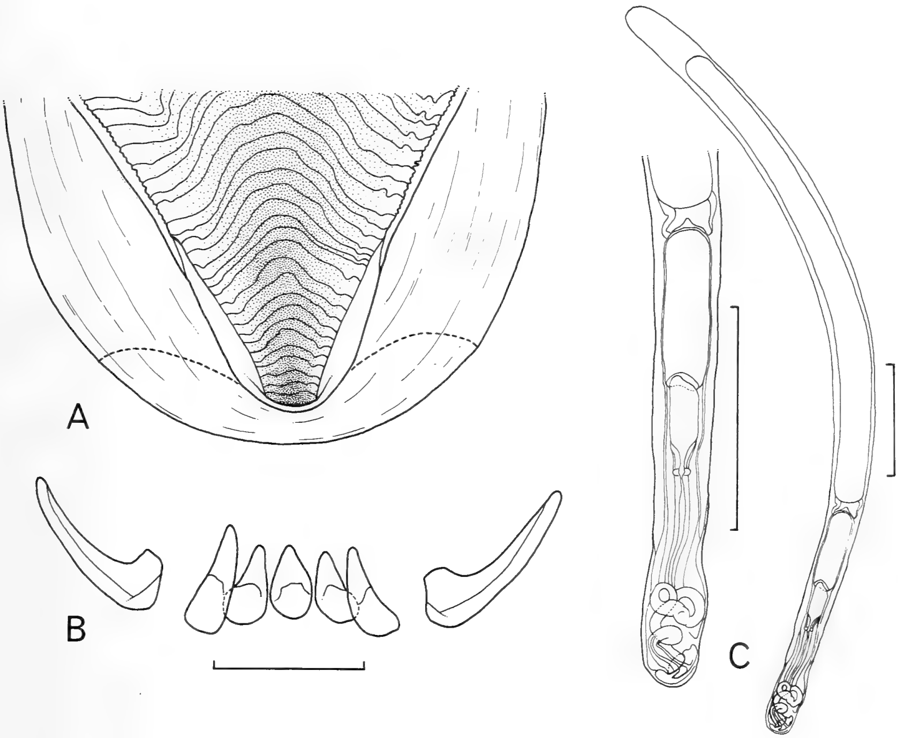

Fig. 9. *Sepia pulchra* sp. nov. A–B. SAM–S1038, ♀ III approx. 19. A. Detail of posterior part of shell, ventral view. B. One row of teeth from radula. C. SAM–S822, ♂ III 22. Spermatophore from Needham's sac, with enlargement of the oral end. Each scale = 0,5 mm.

S. pulchra, the suckers are biserial on arms I–III, with a tendency to irregularity on the lateral arms due to crowding, and quadriserial in the middle of arms IV.

According to Adam & Rees (1966: 119), in the holotype of *S. dubia* 'the dorsal surface of mantle, head and arms is covered with well spaced, round papillae, creating a very rugose appearance. . . . On the dorsal surface of the mantle, approximately in the middle, there are two oval patches of contracted papillae, one on each side of the median line, and a third one anteriorly near the mantle-margin.'

On careful scrutiny, the arrangement of the tubercles of the holotype of *S. dubia* was found to be remarkably like that of *S. pulchra*. The oval patch on either side of the midline in *S. dubia* corresponds with the two main complex tubercles (Fig. 3, a) in *S. pulchra*; the third anterior patch of *S. dubia* is much larger than the corresponding tubercle, c, in *S. pulchra* and may represent an amalgamation of tubercles c and d of *S. pulchra*, as in *S. dubia* there is only this one large tubercle between the two smaller tubercles, g and e, found in both

species. The area of the median tubercles (a–f) does not appear as a distinct dorsal patch in *S. dubia*.

The remaining tubercles (h–s) on the dorsal mantle surface of *S. dubia*, though not very distinct, appear to show the same arrangement as in *S. pulchra*, with the exception of tubercle n. In *S. dubia* tubercle n lies immediately above, rather than in front of, the anterior fin margin, since the distance between the anterior margins of the mantle and the fin is less (12,5% MLd) in *S. dubia* than in *S. pulchra* (23–33% MLd).

At this stage it is not possible to assess the significance of the differences in the tubercles (c, d, n) and the presence or absence of the median patch in separating the two species, since *S. dubia* is known from a single female specimen. However, the two species differ markedly in their shells. *Sepia dubia* has a *Hemisepius*-like shell, with the phragmocone having an inverted triangular shape and occupying little more than half the shell length, as in *Sepia (Hemisepius) typica*. The shell of *S. pulchra*, on the other hand, has an overall resemblance to that of *S. tuberculata,* though being much more fragile; this further weakens the distinction between the subgenera *Sepia* and *Hemisepius*.

AFFINITIES WITH RELATED SPECIES

Sepia pulchra is the fifth small species of *Sepia* to be found in South African waters and further compounds, rather than resolves, the intriguing problem of their interrelationships. The other species are *Sepia robsoni, S. faurei, Sepia (Hemisepius) typica* and *S. (Hemisepius) dubia*. All five species are small, maturing at a dorsal mantle length of about 20 mm. They all have a very broad mantle (MW 60–90% MLd), the anterior margin of which is convex dorsally and deeply emarginate ventrally, and fleshy keels ventrally on the mantle; suckers that are biserial, at least on arms I, II and III; and a tentacular club bearing small subequal suckers and protective membranes that are separate proximally.

Sepia typica, S. dubia and *S. faurei* have a *Hemisepius*-like shell with an abbreviated phragmocone, whereas that of *S. pulchra* is typically sepiid. The shell of *S. robsoni* is virtually unknown. Massy (1927: 160) mentioned only that 'The calcareous portion of the shell has unfortunately been totally dissolved, only the membranous part remaining'. Adam & Rees (1966: 121) found the shell to be in poor condition and compared it to *S. hieronis* and *S. insignis*. If the phragmocone of *S. robsoni* was not of the normal sepiid type, Adam & Rees would certainly have mentioned it.

The convenient separation of these five species into three with a hemisepiid shell and two with a normal shell is not borne out by other characters of the animals. *Sepia robsoni* and *S. faurei* both have dorsal arms with finger-like tips, devoid of suckers, whereas *S. dubia* and *S. pulchra* are virtually indistinguishable at present except by the shell characters.

The resolution of the relationships within this group of five species must await the collection of further specimens of *S. robsoni, S. dubia* and *S. faurei*,

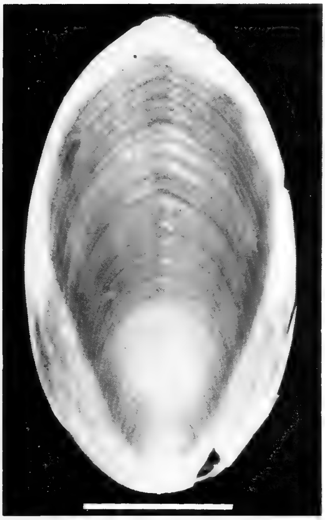

Fig. 10. *Sepia pulchra* sp. nov. Dorsal view of shell of holotype, SAM–S1036, ♂ III 17. Scale = 5 mm.

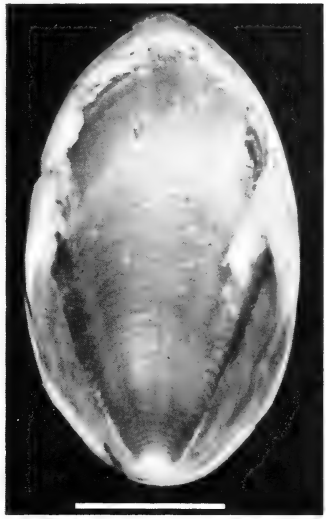

Fig. 11. *Sepia pulchra* sp. nov. Ventral view of shell of holotype, SAM–S1036, ♂ III 17. Scale = 5 mm.

each of which is known only by the holotype. The problem is further complicated by the small size of the animals and the difficulty in extracting the very delicate shells.

BIOLOGICAL OBSERVATIONS

The collection of live specimens of *Sepia pulchra* has provided the opportunity to add a few notes on the biology of the species. The sole, formed by the fleshy keels on the mantle (Fig. 12) and the swollen under-surfaces of the ventral arms, is found in several species (see above), but its use has not been figured before. Since most of the specimens of *S. pulchra* were observed (by W.R.L.) adhering to vertical rock faces in the head-down position, the sole must be of considerable importance in maintaining this position. Camouflage against the background would then be effected by the extensive tuberculation of the dorsal surface of the mantle, head and arms; the well-known ability of sepiids to undergo extreme variation in colour pattern would be a further contributing factor. The reason for the pigmentation of the part of the ventral mantle surface between the keels and fin bases in this species became obvious on observing animals in an aquarium. When an animal adheres to the hard substrate, these parts of the mantle are clearly visible (Fig. 12) and thus also require to be camouflaged, whereas in species that settle on a sandy substrate this part of the mantle is not usually visible.

Two mature males (SAM–S1031) were found to have spermatophores attached to the hectocotylus, allowing the position of the spermatophores to be

Fig. 12. *Sepia pulchra* sp. nov., adhering to rock by fleshy keels of mantle; in this instance the ventral arms are not participating in the adhesion; SAM–S1039, ♀ III 19, photographed in aquarium.

illustrated for the first time (as far as could be established). While copulation has been observed in *S. officinalis* (Grimpe 1926; Bott 1938; Tinbergen 1939), it has been found difficult to see the actual transfer of spermatophores, since this is obscured by the intermingled arms of the mating animals. Bott (1938: 155) has given a detailed description of spermatophore transfer from male to female: the modified (proximal) portion of the hectocotylus, which bears a number of transverse folds on the oral surface bordered by a reduced number of rudimentary suckers, forms a groove connecting the funnel of the male with the bursa copulatrix on the buccal membrane of the female. According to Bott's observations the hectocotylus thus functions as a passage for the spermatophores.

The structure of the hectocotylus of *S. pulchra* is basically like that of *S. officinalis*. However, observations on *S. pulchra* suggest that the spermatophores not only pass along the hectocotylus but are actually attached to the arm (Figs 13–14). Furthermore, Figure 14 shows that the spermatophores are attached to the hectocotylus not only in the ridged area between the rudimentary suckers, but also on the lateral part of the arm outside the sucker rows. Though the attachment of spermatophores to the hectocotylus is not very firm, since the spermatophores are fairly easily dislodged in preserved specimens, the strength of attachment was nevertheless sufficient to maintain the spermatophore position during capture, transport and preservation of these two specimens. The means of attachment of the spermatophores to the hectocotylus would appear to be mucous, since there was no evidence of any structural attachment, nor did the suckers appear to play a part.

Examination of the bundle of spermatophores of *S. pulchra* illustrated in Figure 13 showed the spermatophores to have discharged and be interspersed

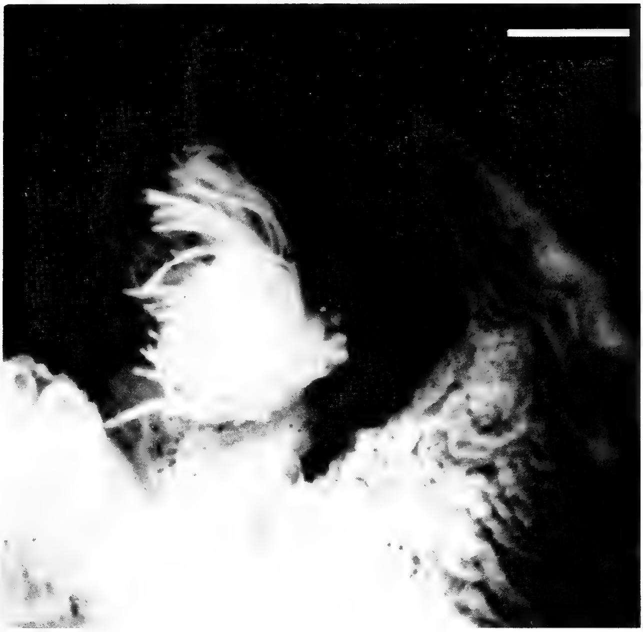

Fig. 13. *Sepia pulchra* sp. nov. Position of spermatophore bundle on modified portion of hectocotylized left ventral arm; SAM–S1031, ♂ III 17. Scale = 2 mm.

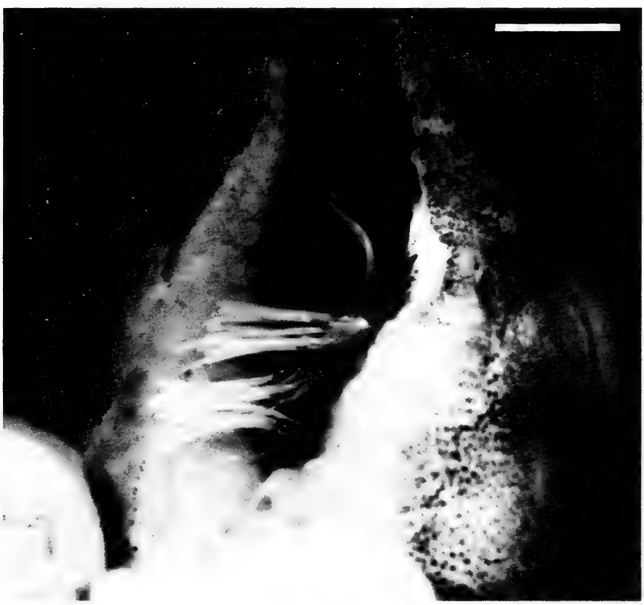

Fig. 14. *Sepia pulchra* sp. nov. Position of individual spermatophores on hectocotylus, after most of spermatophore bundle removed; SAM–S1031, ♂ III 18. Scale = 2 mm.

with sperm reservoirs, the bundle being held together by mucus or perhaps cement from the cement bodies of the spermatophores. The spermatophores in this bundle were all held together by their oral ends, an apparently unnatural condition possibly attributable to the capture and handling of the animal. However, the spermatophores illustrated in Figure 14, which had also ejaculated, were attached to the hectocotylus by their aboral ends, an orientation more consistent with the observation that spermatophores leave the penis aboral-end first and are carried to the female oral-end first, being held in position by the male until the spermatophores have discharged and the sperm reservoirs are fixed by the cement to the female, either in the mantle cavity or on the buccal membrane (Drew 1919: 398, 413).

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
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Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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MARTINA A. ROELEVELD
&
W. R. LILTVED

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[*MS accepted 31 July 1984*]

ABSTRACT

During the second leg of the 1979–Sargasso Sea Expedition, R.V. *Anton Dohrn* occupied a series of stations running south-east of Bermuda to about 25°N and then north-eastwards to the mouth of the English Channel. The MT–1600 and IKMT myctophid samples are analysed independently, using abundances and employing the Bray-Curtis similarity measure with group-average sorting and multi-dimensional scaling ordination. The analyses suggest that for the temperate and subtropical regions of the North Atlantic Ocean, the regional system proposed by Backus *et al*. (1977) is basically accurate, but that the division into North and South Sargasso Sea Provinces requires greater scrutiny, particularly with regard to depth. Indicator species are extracted from the data by the application of information statistic tests. These allow for some comment on community structuring in the geographic regions covered by the transect. The South Sargasso Sea Province is distinguished from the North Sargasso Sea Province by differences in species abundances rather than by differences in faunal structure. The distribution patterns of *Electrona risso, Hygophum benoiti, Benthosema glaciale*, and *Lampanyctus crocodilus* are discussed, those of the latter two species in more detail. It appears that various intraspecific changes do occur across boundary zones, so that the interpretation of these changes should be of prime concern in future investigations of distribution. In conclusion, when catch data are compared with described patterns and subpatterns of distribution, the general rule that species diversity decreases with increasing latitude and that larger populations occur in cold-water species than in warm-water species is confirmed.

CONTENTS

INTRODUCTION

Recent investigations of Atlantic mesopelagic ichthyogeography have culminated in a series of distributional analyses by Parin *et al.* (1974), Krefft (1974, 1978), and Hulley (1981). A system of zoogeographic regions and provinces has been proposed by Backus *et al.* (1977), whose method is based on the conformance of distribution patterns of individual species to selected oceanic physical boundaries.

The aims of this paper are threefold: firstly, to attempt to assess the accuracy of the faunal region and province system, as proposed by Backus *et al.* (1977), in the subtropical-temperate North Atlantic, using the Myctophidae and a method based on abundances; secondly, to examine some of the nuances of myctophid intraspecific change at boundary zones, which may help to justify this system; and thirdly, to hone current ideas on the problematic distribution patterns of some lanternfish species.

MATERIALS AND METHODS

The data used in this analysis are the Myctophidae collected by the R.V. *Anton Dohrn* during the 1979–Sargasso Sea Expedition. The primary objective of this expedition was to investigate aspects of the distribution and biology of eels. The stations occupied are given in Figure 1. During the first leg of the expedition, about 5 000 lanternfish specimens were obtained from the stepped MT–1600, IKMT and MOCNESS hauls (stations AD 23/79 through AD 256/79). The area sampled lay mainly to the south-south-east of Bermuda. The second leg (stations AD 268/79 through 401/79) yielded 15 494 lanternfishes from an MT–1600 transect and 1 715 specimens from IKMT stations, which were occupied during the same transect. The transect ran south-east from Bermuda to about 25°N and then in a north-easterly direction towards the southern entrance of the English Channel (Fig. 1). All material was identified, counted and measured at sea, and representative collections are now housed in the following institutions:

Institut für Seefischerei, Zoologisches Museum, Hamburg (ISH)
Muséum National d'Histoire Naturelle, Paris
National Museum of Natural History, Smithsonian Institution, Washington
South African Museum, Cape Town
Zoologisk Museum, Copenhagen

In addition, data from a series of synoptic neuston tows have been examined (H.-C. John, Zoologisches Museum, Hamburg, pers. comm.).

A description of the XBT sections has been given by Wegner (1979) and the temperature section is reproduced as Figure 12. The hydrographic features for some second-leg stations, AD 265/79 through AD 303/79, are included in the descriptions of the Sargasso Sea in spring 1979 (Wegner 1982).

Data only from the second leg have been used for zoogeographic analysis because of the more extensive area sampled during the transect. Further, since

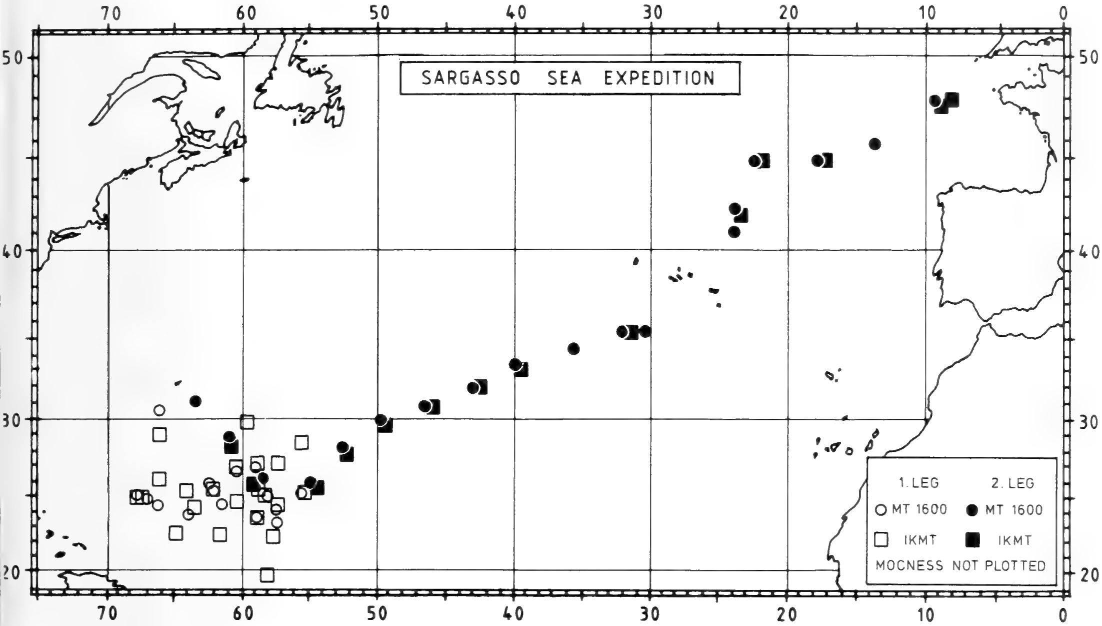

Fig. 1. Station positions for MT–1600 and IKMT hauls for first and second legs of the 1979–Sargasso Sea Expedition of R.V. *Anton Dohrn*. (Note: The 14 IKMT stations from the second leg of the transect are symbolized in this figure; due to the close proximity of certain stations, only 18 of the 38 MT–1600 stations from this leg are depicted; relevant station data are given in Tables 1 and 2.)

both an MT–1600 and an IKMT were deployed, data sets from the two sampling methods could be tested independently. A data matrix of 63 species at 38 stations resulted from the MT–1600 samples, and a data matrix of 33 species at 14 stations from the IKMT samples.

The strategy for analysing marine biological survey data described by Field *et al.* (1982) was used. The methodology is only briefly described below, so that the reader should refer to Field *et al.* (1982) for full details. The advantage of the method is that biotic data are analysed completely separately from environmental data, thereby avoiding any previous assumptions about relationships between biota and environment, cf. Backus *et al.* (1977). The method allows for normal or 'q'-type analysis, in which stations are arranged into groups, each having a similar biotic composition, and inverse or 'r'-type analysis, in which the species are grouped. Further, the application of the information statistic (*I*-) tests to the data matrix provides a means for the recognition of indicator species (Fig. 2).

In the case of the MT–1600 samples, the raw data matrix was scaled to achieve the number of specimens of each species in each haul (station) for a standard period of one hour at fishing depth. The relationship between the computer-generated station numbers and the R.V. *Anton Dohrn* MT–1600

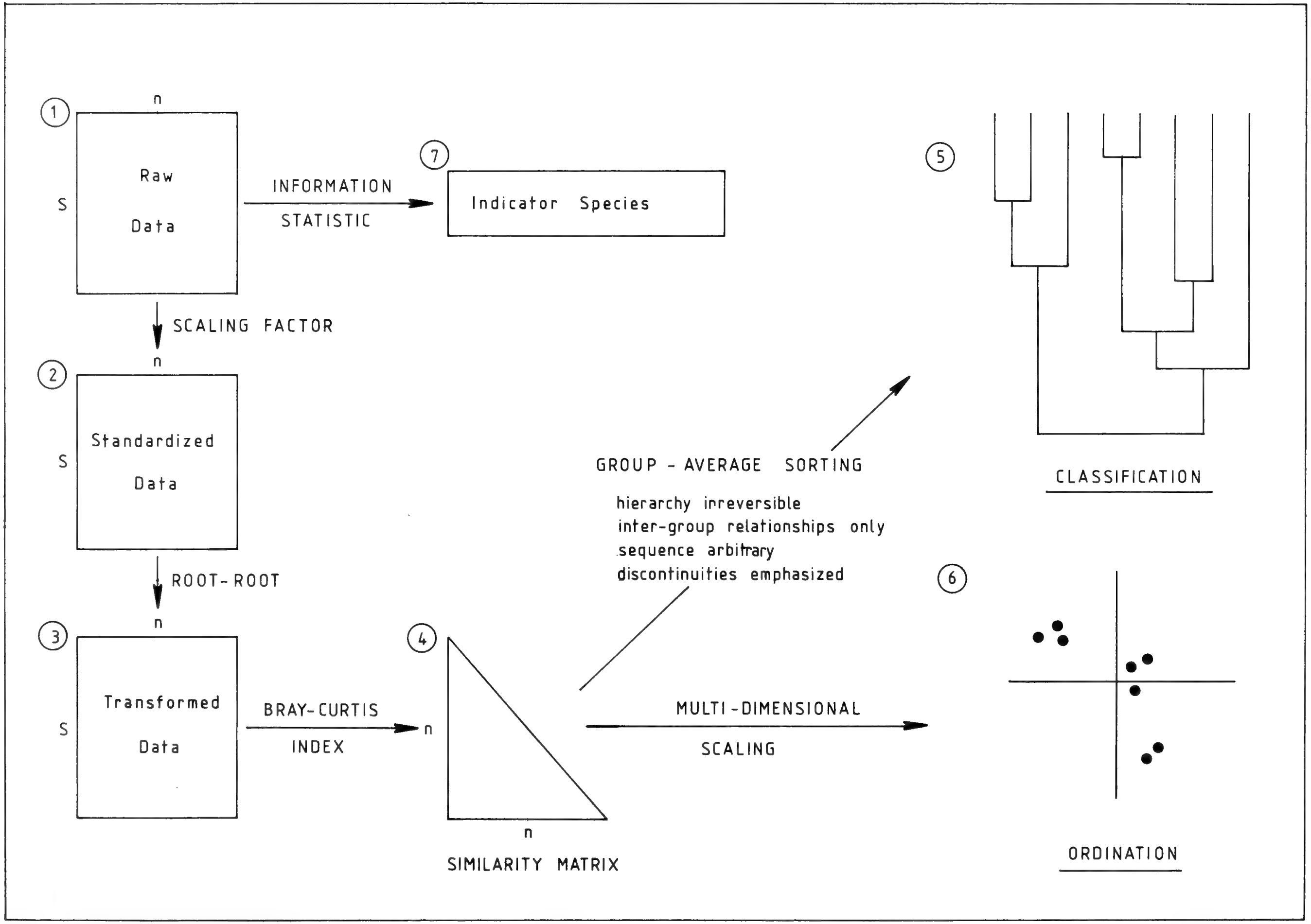

Fig. 2. Flow chart for the Field *et al.* (1982) method of analysis of biological survey data, including disadvantages of group-average sorting.

station numbers is given in Table 1. Since density data are apparently often skewed, in that the abundant species swamp the other data (Field *et al.* 1982), the matrix was root-root transformed. Although the raw data matrix from the IKMT samples was similarly transformed, no scaling factors were employed, because each haul was fished for a standard time and to a similar depth.

The transformed data were then subjected to similarity analysis using the Bray-Curtis measure, resulting in a triangular similarity matrix, whose entries compare each of the samples with every other sample. The technique used to

TABLE 1

1979–Sargasso Sea Expedition (2nd leg). Station list of MT–1600 hauls indicating computer-generated station numbers and their equivalent R.V. *Anton Dohrn* station numbers.

Computer station no.	*AD station no.*	*Position*		*Date*	*Depth* (m)	*Time at depth*
1	268/79	31°11′N	63°27′W	19.04.79	*c.* 1 700	1510–1555
2	269/79	30°05′N	63°23′W	19.04.79	170	1944–1959
3	270/79	31°01′N	63°15′W	19.04.79	250	2055–2110
4	276/79	28°41′N	60°54′W	20.04.79	*c.* 1 800	1510–1600
5	284/79	26°11′N	58°26′W	21.04.79	2 000	1500–1600
6	293/79	25°49′N	54°58′W	22.04.79	*c.* 2 000	1505–1600
7	301/79	27°38′N	52°22′W	23.04.79	2 000	1455–1545
8	302-I/79	27°49′N	52°13′W	23.04.79	300	1915–1928
9	308/79	29°40′N	49°38′W	24.04.79	*c.* 2 000	1535–1630
10	309-I/79	29°41′N	49°27′W	24.04.79	110	1917–1932
11	314-I/79	30°43′N	46°16′W	25.04.79	2 000	1637–1735
12	314-II/79	30°45′N	46°08′W	25.04.79	195	2015–2030
13	315/79	30°47′N	46°04′W	25.04.79	306	2110–2125
14	321/79	31°51′N	42°55′W	26.04.79	1 950	1630–1725
15	322/79	31°53′N	42°48′W	26.04.79	190	2002–2017
16	323/79	31°55′N	42°46′W	26.04.79	380	2057–2112
17	329/79	32°59′N	39°41′W	27.04.79	1 950	1535–1630
18	330/79	33°01′N	39°34′W	27.04.79	185	1955–2010
19	331/79	33°04′N	39°29′W	27.04.79	345	2050–2110
20	338/79	34°21′N	35°29′W	28.04.79	1 300	1700–1800
21	339/79	34°20′N	35°24′W	28.04.79	170	2040–2055
22	340/79	34°21′N	35°22′W	28.04.79	320	2133–2148
23	345/79	35°24′N	32°01′W	29.04.79	1 800	1700–1750
24	346-I/79	35°24′N	31°53′W	29.04.79	350	2030–2045
25	348/79	35°20′N	30°16′W	30.04.79	*c.* 1 900	0640–0710
26	361/79	41°02′N	23°52′W	02.05.79	>2 000	1135–1230
27	364/79	42°05′N	23°30′W	02.05.79	155	2020–2035
28	365/79	42°06′N	23°29′W	02.05.79	340	2110–2125
29	371/79	44°54′N	22°16′W	03.05.79	2 000	1638–1730
30	372/79	44°56′N	22°00′W	03.05.79	175	2022–2037
31	373/79	44°56′N	21°57′W	03.05.79	340	2113–2128
32	380/79	44°55′N	17°34′W	04.05.79	2 000	1720–1820
33	381/79	44°55′N	17°22′W	04.05.79	205	2100–2115
34	382/79	44°56′N	17°18′W	04.05.79	*c.* 350	2204–2219
35	389/79	45°41′N	13°42′W	05.05.79	*c.* 2 000	1713–1810
36	390/79	45°54′N	13°30′W	05.05.79	205	2044–2059
37	391/79	45°55′N	13°27′W	05.05.79	350	2136–2151
38	398/79	47°42′N	09°08′W	06.05.79	2 000	1837–2000

produce the dendrogram from the similarity matrix was group-average sorting, which joins two groups of samples together at the average level of similarity between all members of one group and all members of the other.

While dendrograms have the advantage of simplicity, they have a number of disadvantages (*fide* Fig. 2), so that a multi-dimensional scaling (MDS) method of ordination was also employed. This seeks to reconcile the interstation distances in a specified number of dimensions in ordinary Euclidean space, with the physical distances between points on a two-dimensional map.

RESULTS AND DISCUSSION

Normal ('q'-type) analysis

The dendrogram given in Figure 3 shows station affinities based on the root-root transformed abundances of all 63 species of Myctophidae taken during the MT–1600 transect. The broken line drawn at the arbitrary similarity level of 20 per cent delineates two major groups of stations, while the broken line drawn at the arbitrary similarity level of 40 per cent delimits three groups of stations:

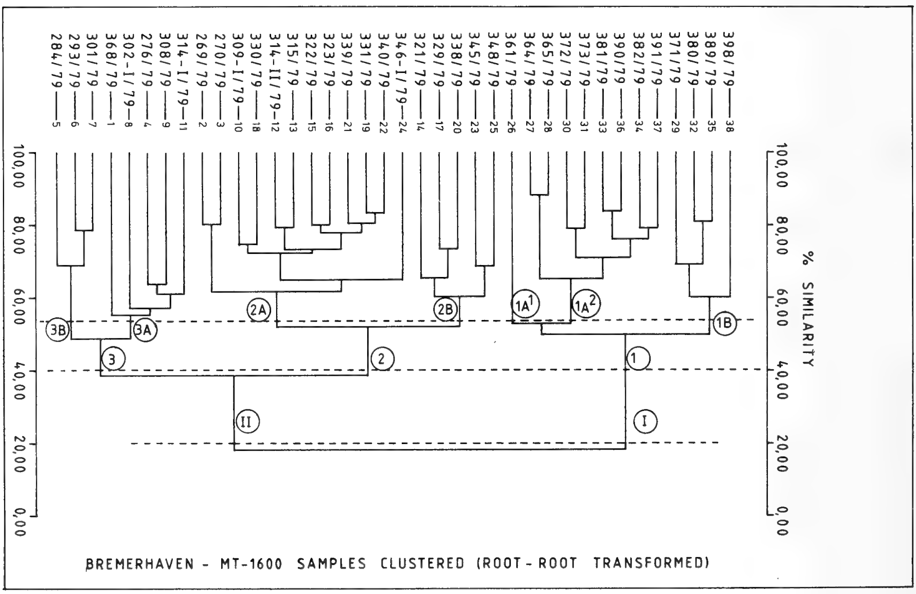

Fig. 3. Dendrogram for station affinities for MT–1600 hauls.

Group 1: which subsequently divides into three sub-groups at the 54 per cent similarity level (arbitrary choice), designated Groups 1A^1, 1A^2 and 1B (Fig. 3).

Groups 2 and 3: which are more closely related to each other than to Group 1, and which both divide into two sub-groups, also at the 54 per cent

similarity level, designated Groups 2A and 2B and Groups 3A and 3B, respectively.

The ordination of the similarity matrix using MDS (Fig. 4) gives the same groupings as the dendrogram (Fig. 3). Attention should be directed to the proximity of the two stations numbered 8 (in Group 3A) and 26 (in Group $1A^1$),

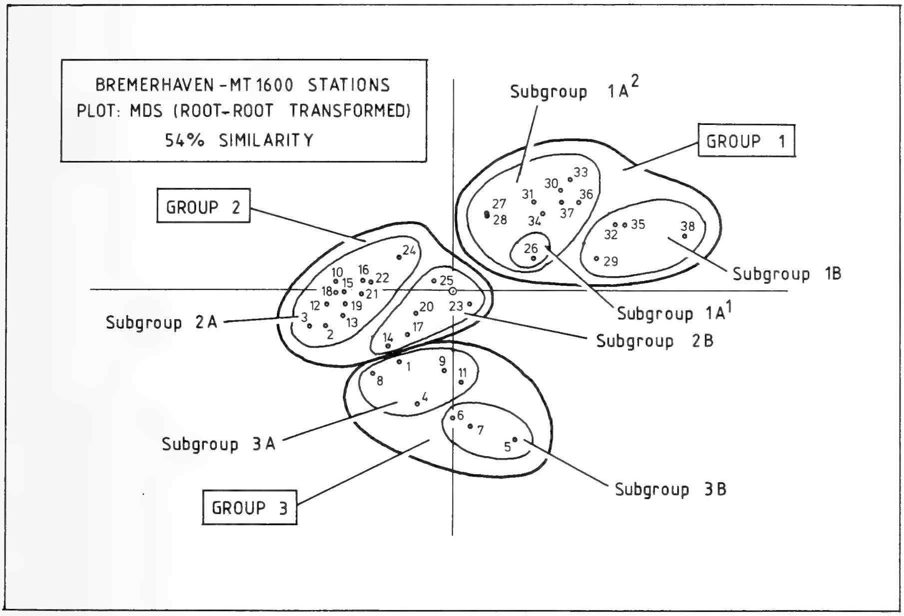

Fig. 4. MDS ordination of MT–1600 station affinities.

to Groups 2A and 1B respectively. In order to check that the dendrogram is not an artifact of the standardization employed in the manipulation of the raw data matrix, the scaling factors have been superimposed on the MDS ordination (Fig. 5). There appears to be no marked correlation, as is evident from the numerous anomalies. The correlation appears to be somewhat better if daylight and night data are superimposed on the ordination (Fig. 6). However, since the sampling programme on board was such that the deep stations were usually fished during the day and shallower stations usually at night, depth data have been superimposed on the ordination (Fig. 7) and result in the best correlation:

1. All Group $1A^2$ stations are shallow hauls; all Group 1B stations are deep hauls; and the single station in Group $1A^1$ (Station 26), a deep haul, has a close affinity to the deep-haul stations of Group 1B.

2. Group 2A stations are all shallow hauls, while Group 2B stations are all deep hauls.

3. Of the stations in Group 3, Station 8 (shallow haul) has a close affinity with the shallow-haul stations of Group 2A.

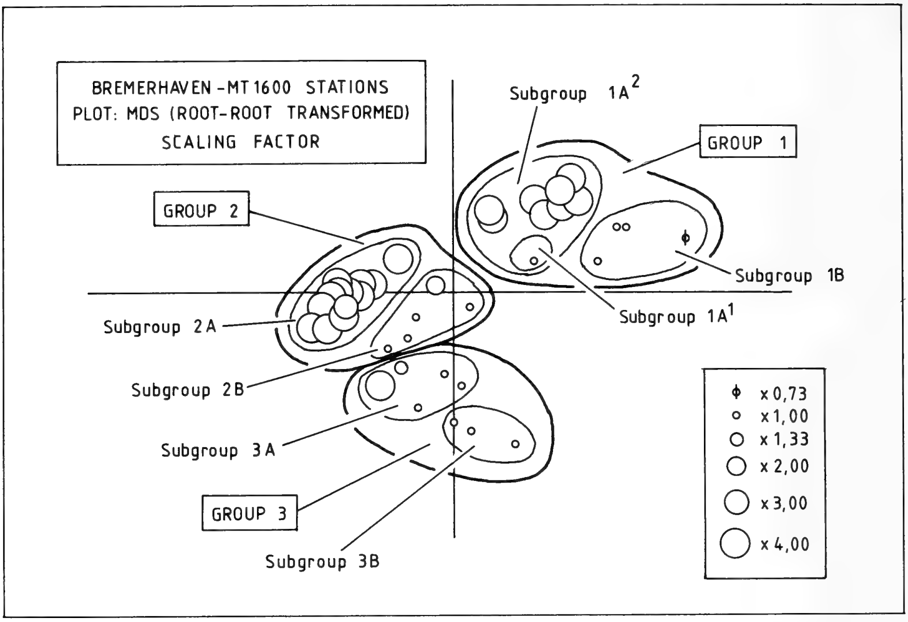

Fig. 5. Scaling factors superimposed on MDS ordination for MT–1600 hauls.

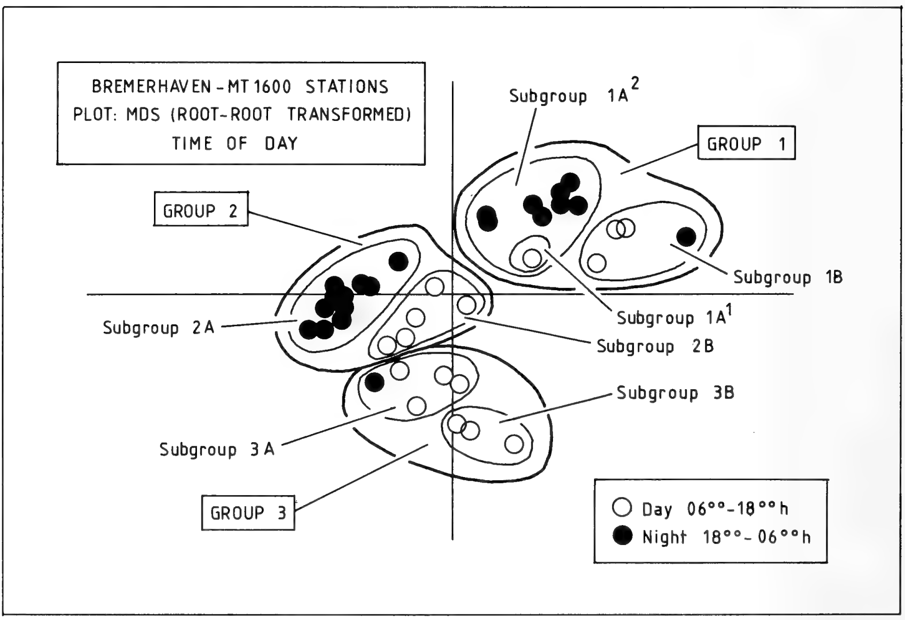

Fig. 6. Day and night data superimposed on MDS ordination for MT–1600 hauls.

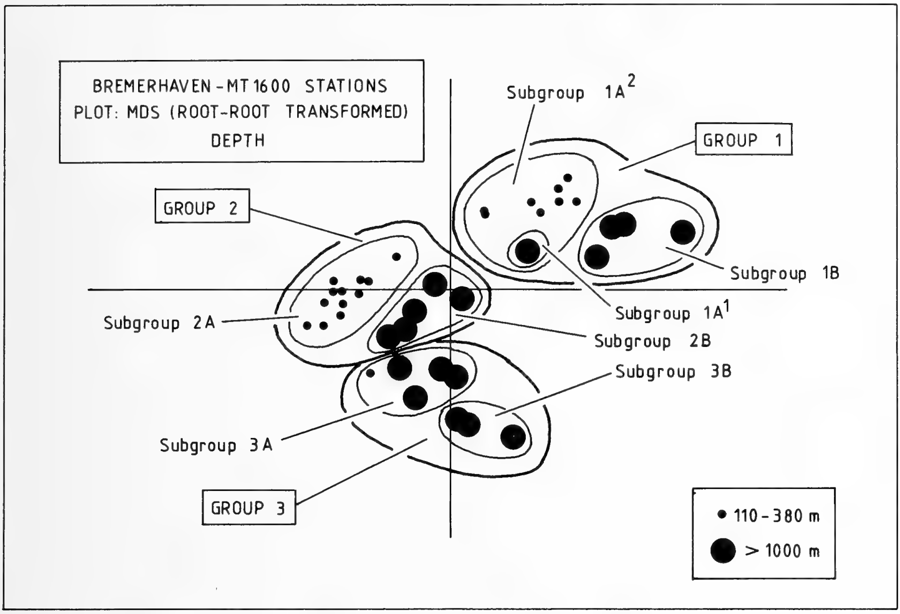

Fig. 7. Depth data superimposed on MDS ordination for MT–1600 hauls.

Geographic plots of these station groupings in terms of the Backus *et al.* (1977) regional system (Fig. 8) reveal that:

(i) Group 1 stations are all found to the north of the proposed boundary between the Temperate Region and the Subtropical Region, i.e. the 15 °C isotherm at 200 m. They are Temperate Region stations, and both deep- and shallow-haul stations belong to this group.

(ii) Group 2 stations are, in the main, found in the North Sargasso Sea Province and the North North African Subtropical Sea Province. They are Subtropical Region stations and are closely associated with Group 3 stations.

(iii) Group 3 stations are in the main in the South Sargasso Sea Province, with Group 3B representing the most southerly stations of the transect.

Of interest is the fact that at three geographical positions, both Group 2 and Group 3 elements are present. The analysis shows that in each case the shallow-haul stations are related to Group 2, i.e. they are subtropical, while the deeper-haul stations are related to Group 3. This will be discussed below.

A similar procedure was followed for the IKMT data, but was less complicated due to the fact that all hauls were at night and to about 200 m. The relationship between the computer-generated station numbers and the R.V. *Anton Dohrn* IKMT station numbers is given in Table 2. Figure 9 is the dendrogram of the station affinities, based on root-root transformed abundances of 33 species of Myctophidae taken at 14 stations. The broken line drawn at the arbitrary similarity levels of both 20 per cent and 40 per cent delimits two major

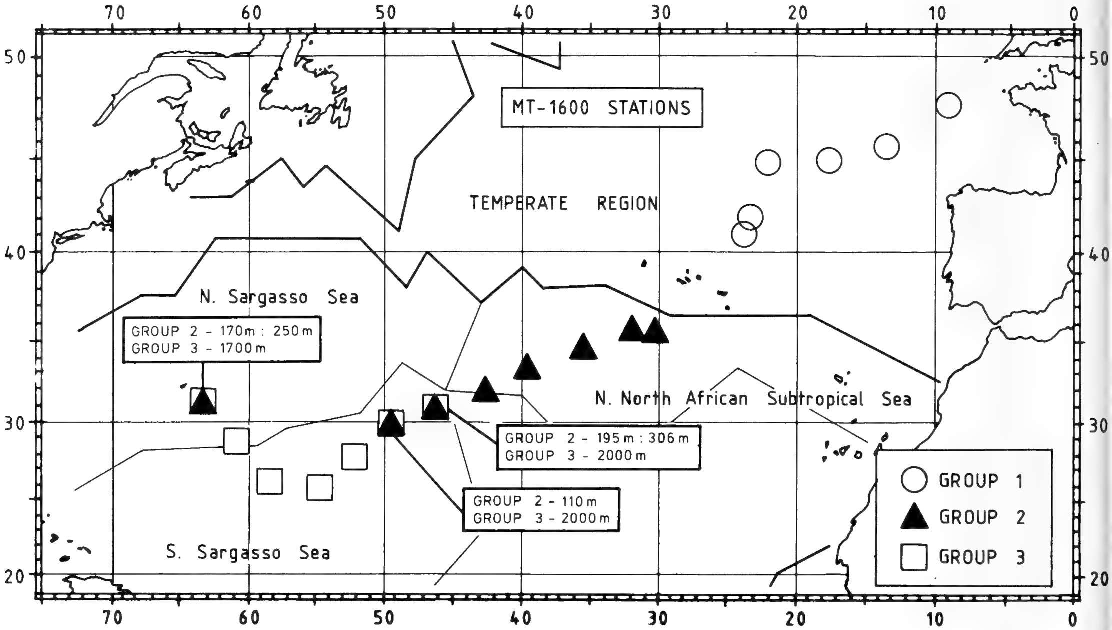

Fig. 8. Geographic plots of MT–1600 hauls showing distribution of Groups 1, 2, and 3.

TABLE 2

1979–Sargasso Sea Expedition (2nd leg). Station list of IKMT hauls indicating computer-generated station numbers and their equivalent R.V. *Anton Dohrn* station numbers.

Computer station no.	*AD station no.*	*Position*		*Date*
1	277/79	28°20′N	60°33′W	20.04.79
2	286/79	25°52′N	58°12′W	21.04.79
3	294/79	25°49′N	54°31′W	22.04.79
4	302-II/79	27°51′N	52°11′W	23.04.79
5	309-II/79	29°41′N	49°27′W	24.04.79
6	316/79	30°48′N	46°02′W	25.04.79
7	324/79	31°56′N	42°43′W	26.04.79
8	332/79	33°04′N	29°34′W	27.04.79
9	346-II/79	35°23′N	31°51′W	29.04.79
10	366/79	42°07′N	23°29′W	02.05.79
11	374/79	44°56′N	21°55′W	03.05.79
12	383/79	44°56′N	17°17′W	04.05.79
13	399/79	47°44′N	08°58′W	06.05.79
14	401/79	47°58′N	08°16′W	07.05.79

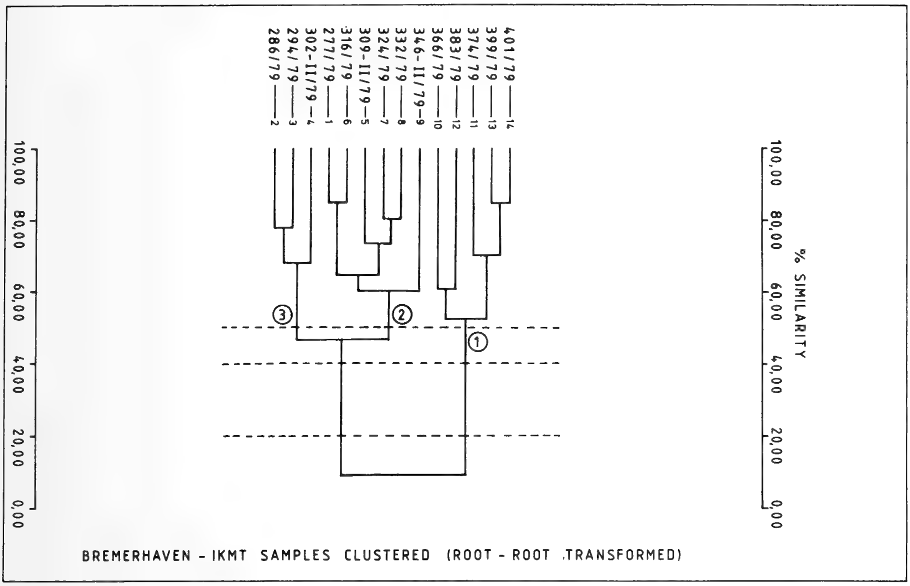

Fig. 9. Dendrogram for station affinities for IKMT hauls.

groups of stations, while the broken line drawn at the arbitrary similarity level of 50 per cent delimits three groups of stations, designated Groups 1, 2 and 3. The MDS ordination plots for the IKMT stations (Fig. 10) support this and demonstrate further that Groups 2 and 3 have a closer affinity to each other than either to Group 1. The geographical plots of the IKMT groupings (Fig. 11) support not only the results obtained from the analysis of the MT–1600 samples, but also support the ideas regarding the affinities of those stations immediately adjacent to the boundaries between the provinces of the Subtropical Region. That is, these shallow hauls show an affinity with the North Sargasso Sea or North North African Subtropical Sea Provinces within the boundaries proposed by Backus *et al.* (1977), while Group 3 stations are well within the South Sargasso Sea Province.

Examination of the temperature section for the transect (Fig. 12) reveals that there are three main hydrographic features:

1. Stations AD 275/79 through AD 305/79 are characterized by the presence of water warmer than 20 °C in the upper 50 m; by a layer of '18 °C water' between 200 m and about 400 m, the intermediate layer of the whole Sargasso Sea Region (Wegner 1979); and by the position of the 15 °C isotherm below about 500 m. These stations cover the region of the warm South Sargasso Sea Water. While Wegner (1982) points out that the convergence area is demarcated by the 21 °C and 22 °C isotherms in depths of 100 m, this feature is not well defined over the MT–1600 transect (Fig. 12; Wegner 1982, fig. 3a), due to the fact that there is a masking layer of transition water to the north. A similar condition appears to be

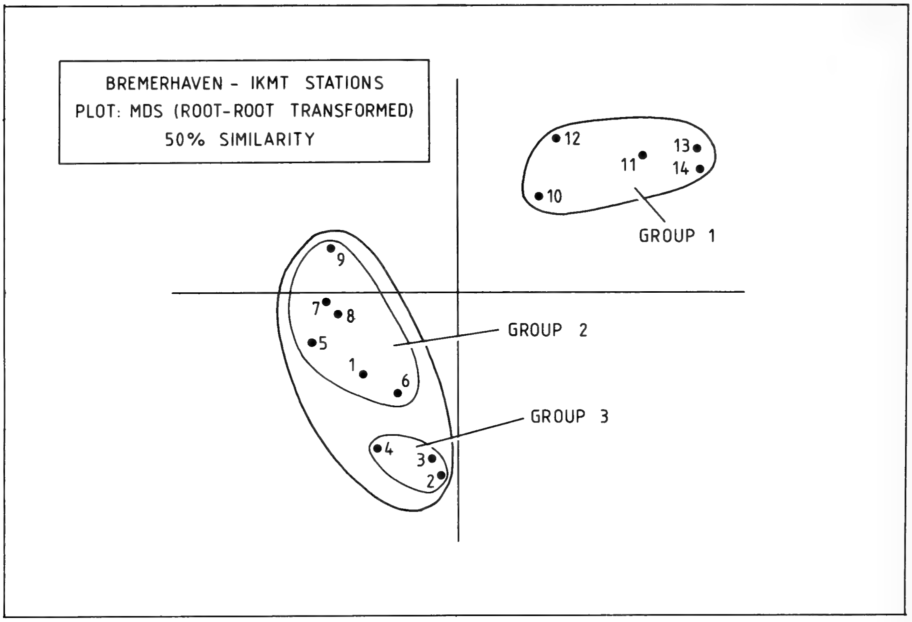

Fig. 10. MDS ordination of IKMT station affinities.

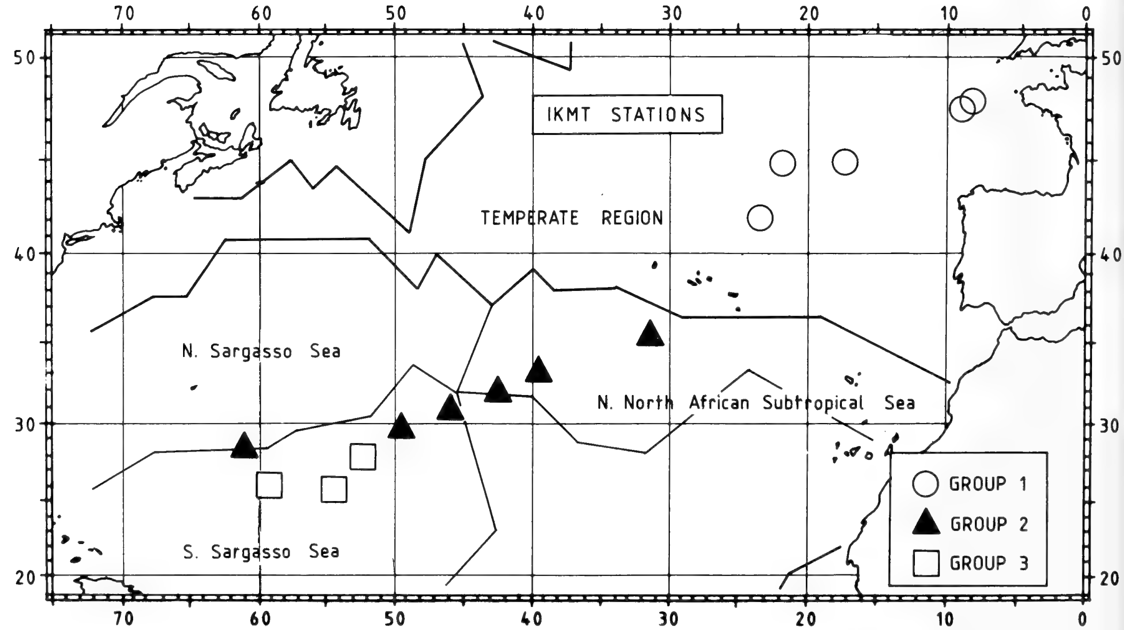

Fig. 11. Geographic plots of IKMT hauls showing distribution of Groups 1, 2, and 3.

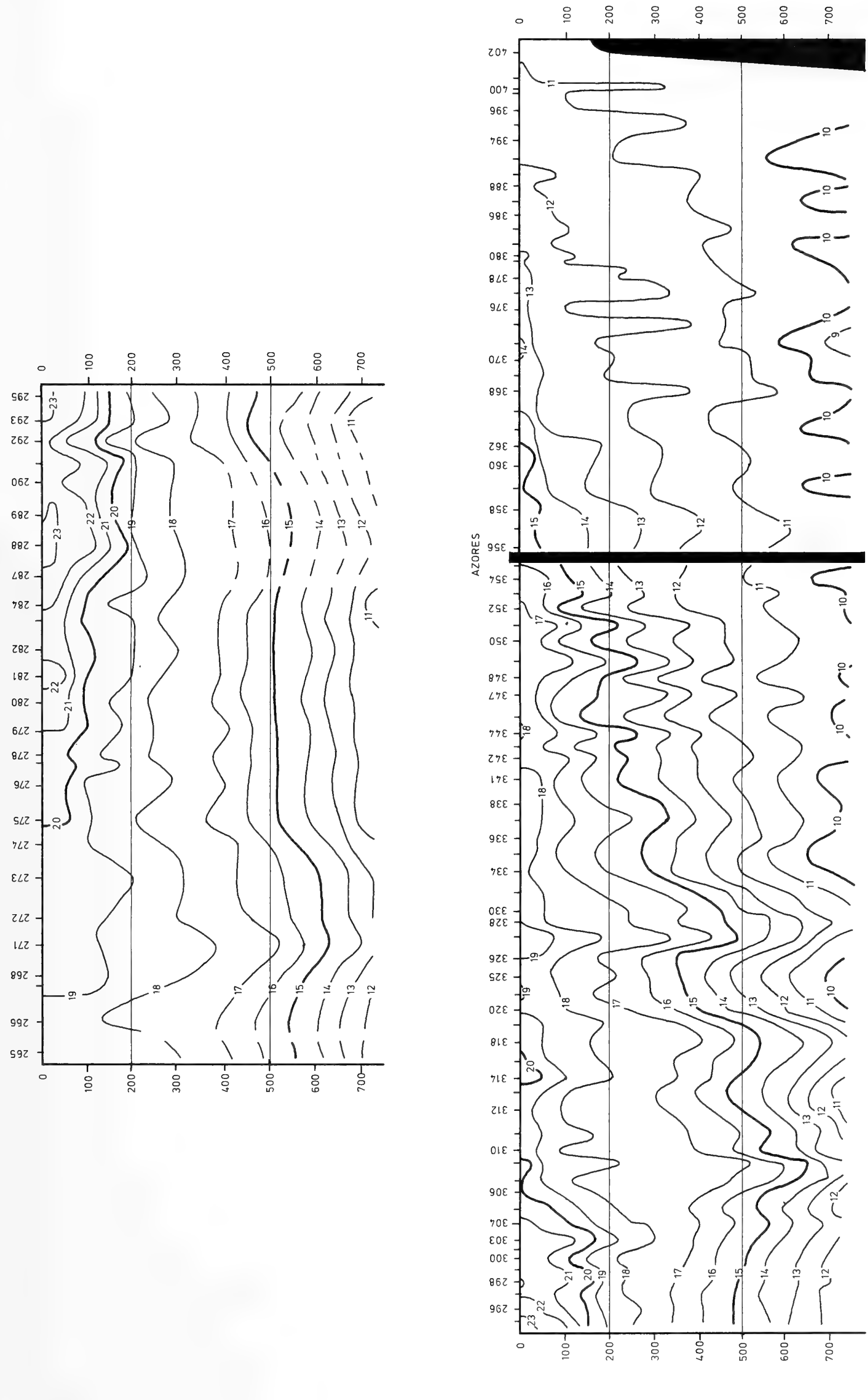

Fig. 12. Temperature section of the second leg of the 1979–Sargasso Sea Expedition (after Wegner 1979).

evident over that region which includes stations AD 306/79 through AD 318/79. Unfortunately, salinity distribution, which usually gives a better resolution for convergence determination, gave only the surface distribution across this transect (Wegner 1982). South Sargasso Sea Water probably occurred from about AD 279/79 to AD 306/79. On the basis of the biological analysis, the stations from this region represent those of Group 3.

2. Stations AD 321/79 through AD 351/79 are characterized by water of 17–19 °C, which replaces the warm South Sargasso Sea Water (>20 °C) in the upper 150 m; the absence of '18 °C water' in depths of 200 m to 400 m; the position of the 15 °C isotherm between 200 m and 500 m; and the position of the 11 °C isotherm in depths below 500 m (550–650 m). Group 2 stations are found over this region of the transect.

3. Stations AD 352/79 through AD 403/79, which include the biological sampling stations AD 361/79 to AD 401/79, are characterized by the position of the 15 °C isotherm in depths shallower than 200 m; and by the position of the 11 °C isotherm in depths shallower than about 500 m. The biological grouping of these stations is Group 1.

A summary of these relationships is given in Table 3.

TABLE 3

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Relationships of the myctophid MDS-ordination analysis to temperatures at depth.

Depth (m)	*Temperatures* (°C)		
	Group 1	*Group 2*	*Group 3*
100	<15	15–19	>20
500	<11	12–15	>15

As has been pointed out above, at certain geographic positions (AD 268/79–270/79; AD 308/79–309-I/79; AD 314-I/79–315/79) both Group 2 stations (hauls to 250 m) and Group 3 stations (hauls below 1 700 m) were present. As can be seen in Figure 12, the temperature profiles at these positions reveal that, while the 15 °C isotherm lies below 500 m and there is '18 °C water' between 200 m and 400 m, conditions that approximate those for Group 3 stations, the temperature regime in the upper 200 m is characteristic of Group 2 stations, i.e. those of the North Sargasso Sea and North North African Subtropical Provinces and the transition zones immediately adjacent to the convergence. The inclusion of the MT–1600 station, AD 276/79 (*c.* 1 800 m), of Group 3, with the adjacent IKMT–station, AD 277/79 (100 f.w.o.) of Group 2, would tend to support the temperature parameters suggested above, particularly if the position of the convergence is defined according to Wegner's (1982) criteria.

The groupings for the shallow-haul stations from both the MT–1600 and the IKMT transects have been amalgamated and isohalines at 200 m, taken from Wüst & Defant (1936), have been superimposed on a geographical plot (Fig. 13), in order to elucidate relationships of these groups to salinity. The relationship of the Group 3 stations to the region of high salinity is fairly good. Since the lens of

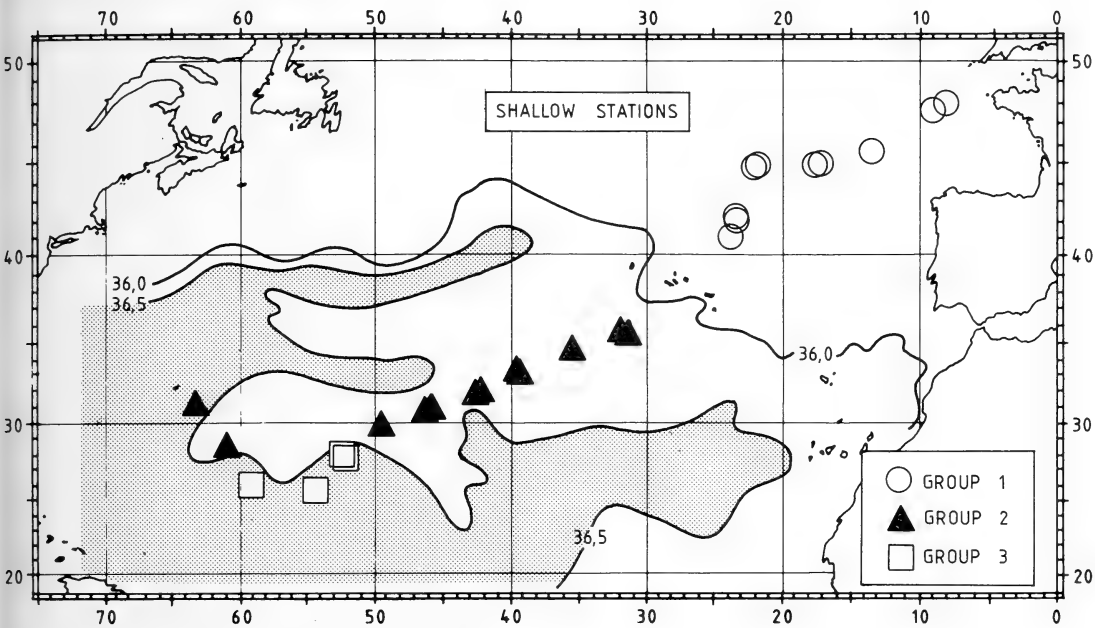

Fig. 13. Geographic plots of shallow stations (MT–1600 and IKMT) in relation to isohalines, from Wüst & Defant (1936).

high-temperature and high-salinity water at the gyral-eye is inclined from 200 m in the west to 800–1 000 m in the east, and since this warm, saline water extends farther to the east and north-east at greater depths than at shallower depths (as indicated by isohaline examination in Wüst & Defant 1936), the above interpretation of these data may be correct.

Indicator species and community structure

In discussing these topics with regard to the 1979–transect, several facts should be borne in mind. Firstly, $2\Delta I_i$ has approximate chi-square distribution but lacks statistical rigour (Field *et al.* 1982). The scores of $2\Delta I_i > 3{,}84$ (5% probability level) and $2\Delta I_i > 6{,}63$ (1% probability level) are therefore only employed as a 'rule of thumb' for the cut-off limits. Secondly, it is evident to us that certain small species (*Diogenichthys atlanticus* and *Notolychnus valdiviae*) and surface migrators (*Gonichthys cocco, Myctophum nitidulum*, and *Symbolophorus rufinus*) are not well represented in MT–1600 samples. This may be due

to the mesh size in front of the cod-end liner of the MT–1600, or the fact that on hauling the MT–1600 collapses just below the surface, or both. Other species (*Lampadena anomala, Loweina interrupta*, and *Loweina rara*) may indeed be uncommon. Thirdly, our data result from a single transect. Therefore seasonal changes in distributional range and seasonal variability in myctophid community structure cannot be discussed. Unpublished data from more recent cruises have indicated that this may be of importance, e.g. in *Bolinichthys supralateralis, Diaphus dumerilii*, and *Lampadena urophaos atlantica*. Finally, and in addition to its known inefficiency in sampling the myctophid fauna, the IKMT was fished only to 200 m, thereby biasing the results for the deeper-living species (*Lampanyctus crocodilus* and *L. photonotus*). Only about half (52,38 %) of the species caught by the MT–1600 are represented in the IKMT samples. Therefore a table of the indicator species only is presented for the IKMT data (Table 8).

Results of information statistic (*I*-) tests for the MT–1600 data, which are calculated from the numbers of specimens (density), are presented in Tables 4, 5 and 6. Table 4 lists the species that are characteristic of Group 1 and distinguish them from combined species of Group 2 and Group 3. There are no 'perfect' indicator species. That is, there are no species that occur in all samples of Group 1 and in none of the samples of the compared groups. However, all those species listed may be considered to be indicators, whose presence or absence at stations

TABLE 4

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence (F) and numbers of individuals (N) of species, ranked according to information statistics, which distinguish Group 1 (F_1, N_1) from Groups 2 and 3 (F_{2+3}, N_{2+3}). $2\triangle I_i$ values are calculated from numbers of specimens. Species above horizontal dotted line have $2\triangle I_i > 6{,}63$; those below line have $2\triangle I_i > 3{,}84$; species with $2\triangle I_i < 3{,}84$ are not included. Maximum values for F_1 and F_{2+3} are given in parentheses.

Species	F_1 (13)	N_1	F_{2+3} (25)	N_{2+3}	$2\triangle I$
Benthosema glaciale	13	11 698	1	4	25 026,911
Notoscopelus kroeyerii	12	7 163	0	0	15 366,595
Myctophum punctatum	12	1 969	1	4	4 169,793
Ceratoscopelus maderensis	10	613	3	70	922,185
Symbolophorus veranyi	11	494	6	32	845,378
Notoscopelus bolini	5	743	8	187	817,022
Electrona risso	12	437	3	21	784,590
Diaphus holti	11	394	2	46	588,997
Lampanyctus crocodilus	13	285	4	10	532,432
Diaphus rafinesquii	12	458	14	380	146,311
Lampanyctus intricarius	10	55	0	0	117,990
Lampanyctus macdonaldi	3	14	0	0	30,034
Lampadena speculigera	5	11	0	0	23,598
Protomyctophum arcticum	4	11	0	0	23,598
Loweina interrupta	1	4	0	0	8,581
....					
Diaphus metopoclampus	4	14	4	10	5,807

within the group is a function of their geographic range and/or vertical distribution pattern, e.g. *Lampanyctus macdonaldi* and *Protomyctophum arcticum*. Comparison of the frequencies of occurrence within (F_1) and outside (F_{2+3}) the group is an expression of fidelity; that is, the degree of exclusiveness that the species shows towards Group 1 (Temperate Region community), while numbers

TABLE 5

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence (F) and numbers of individuals (N) of species, ranked according to information statistics, which distinguish Group 2 (F_2, N_2) from Groups 1 and 3 (F_{1+3}, N_{1+3}). Other conventions as in Table 4.

Species	F_2 (17)	N_2	F_{1+3} (21)	N_{1+3}	$2 \triangle I$
Ceratoscopelus warmingii	17	4 944	8	155	6 826,668
Hygophum hygomii	17	4 214	10	134	5 741,827
Lobianchia gemellarii	17	4 287	19	428	4 534,569
Hygophum benoiti	16	2 708	5	368	2 540,122
Lobianchia dofleini	16	2 166	5	198	2 358,445
Diaphus mollis	15	1 327	7	57	1 727,171
Bolinichthys indicus	17	1 474	12	292	1 133,791
Notoscopelus resplendens	17	625	1	13	893,924
Lampanyctus photonotus	16	790	11	90	796,776
Lampandena urophaos atlantica	11	371	4	6	542,372
Lepidophanes gaussi	14	447	4	37	501,633
Notoscopelus caudispinosus	16	331	5	18	412,061
Benthosema suborbitale	10	222	0	0	357,142
Lampadena chavesi	11	208	0	0	334,619
Lampanyctus festivus	14	178	2	6	240,593
Hygophum reinhardtii	15	208	4	16	238,318
Diaphus effulgens	8	142	2	5	190,735
Taaningichthys minimus	12	153	5	12	174,361
Diogenichthys atlanticus	12	101	1	1	152,429
Lampanyctus pusillus	17	863	14	566	140,861
Lampanyctus ater	13	227	9	62	138,223
Lepidophanes guentheri	8	142	4	21	128,113
Diaphus lucidus	8	64	0	0	102,960
Diaphus splendidus	6	60	0	0	96,525
Diaphus brachycephalus	7	72	1	3	94,196
Loweina rara	6	37	0	0	59,524
Diaphus problematicus	3	32	0	0	51,480
Diaphus perspicillatus	3	31	1	1	42,157
Notolychnus valdiviae	3	26	0	0	41,827
Myctophum selenops	7	45	2	9	34,408
Diaphus dumerilii	4	21	0	0	33,784
Hygophum taaningi	2	48	4	14	27,590
Bolinichthys photothorax	2	11	0	0	17,696
Centrobranchus nigroocellatus	2	5	0	0	8,004
Diaphus bertelseni	2	5	0	0	8,004
Lampanyctus lineatus	7	26	5	14	6,637
....					
Diaphus termophilus	1	4	0	0	6,435
Lampanyctus nobilis	1	4	0	0	6,435
Lampanyctus alatus	1	4	0	0	6,435

TABLE 6

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence (F) and numbers of individuals (N) of species, ranked according to information statistics, which distinguish Group 3 (F_3, N_3) from Groups 1 and 2 (F_{1+2}, N_{1+2}). Other conventions as in Table 4.

Species	F_3 (8)	N_3	F_{1+2} (30)	N_{1+2}	$2\Delta I$
Lampanyctus cuprarius	8	184	13	126	214,132

of individuals (N_1) are indicative of their relative abundance. A plot of cumulative percentage densities for those ranked species with $2\Delta I_i > 6{,}63$ (Fig. 14) reveals that 5 species (*Benthosema glaciale, Notoscopelus kroeyerii, Myctophum punctatum, Notoscopelus bolini*, and *Ceratoscopelus maderensis*) are dominant and comprise about 90 per cent of the total. The N_1 and N_{2+3} values for *Notoscopelus bolini* are high, and the sampled material consists mainly of very small juvenile specimens (SL 24–42 mm). Only a single adult specimen (SL 92 mm) of this species was taken during the transect (in the Group 1 area). A similar bias is evident in the IKMT samples (see below). Shannon diversity indices (H) for the Group 1 stations (MT–1600 samples) were calculated using:

$$H = \frac{n \log_{10} n - \sum_{i=1}^{k} f_i \log_{10} f_i}{n}$$

H values ranged between 0,42 and 1,12 (Table 7). Of the 15 species (with $2\Delta I_i > 6{,}63$) involved in this community, 10 are endemic to the temperate North Atlantic, 4 possess a Bitemperate Pattern and 1 species, *Electrona risso*, is said to have either an Eastern Pattern (Backus *et al.* 1977) or a Widespread Pattern (Hulley 1981). Two genera are represented by 2 species each (*Diaphus holti, D. rafinesquii, Notoscopelus bolini*, and *N. kroeyerii*) and one genus by 3 species (*Lampanyctus crocodilus, L. intricarius*, and *L. macdonaldi*). In relation to niche separation, data from the 1982–Mid-Atlantic Ridge and 1983–TIFI–8 cruises indicate possible differences in spawning season and a noticeable degree of vertical separation of adult specimens of the *Lampanyctus* species, while *Notoscopelus kroeyerii* may well have to be re-assessed as a pseudoceanic species (unpublished data). Comment on the association of *Diaphus holti* with Mediterranean Outflow Water has already been made (Hulley 1981).

Similarly, Table 5 lists those species that are characteristic of Group 2 and distinguish it from Groups 1 and 3. Again, there are no 'perfect' indicator species for the group, but *Notoscopelus resplendens* is always present in Group 2 and occurs very rarely (only once, with 13 specimens) in the other groups. There are only 5 species that are endemic to the Atlantic; 19 species have Broadly Tropical Patterns, 11 have Subtropical Patterns, 5 have Tropical Patterns, 3 have

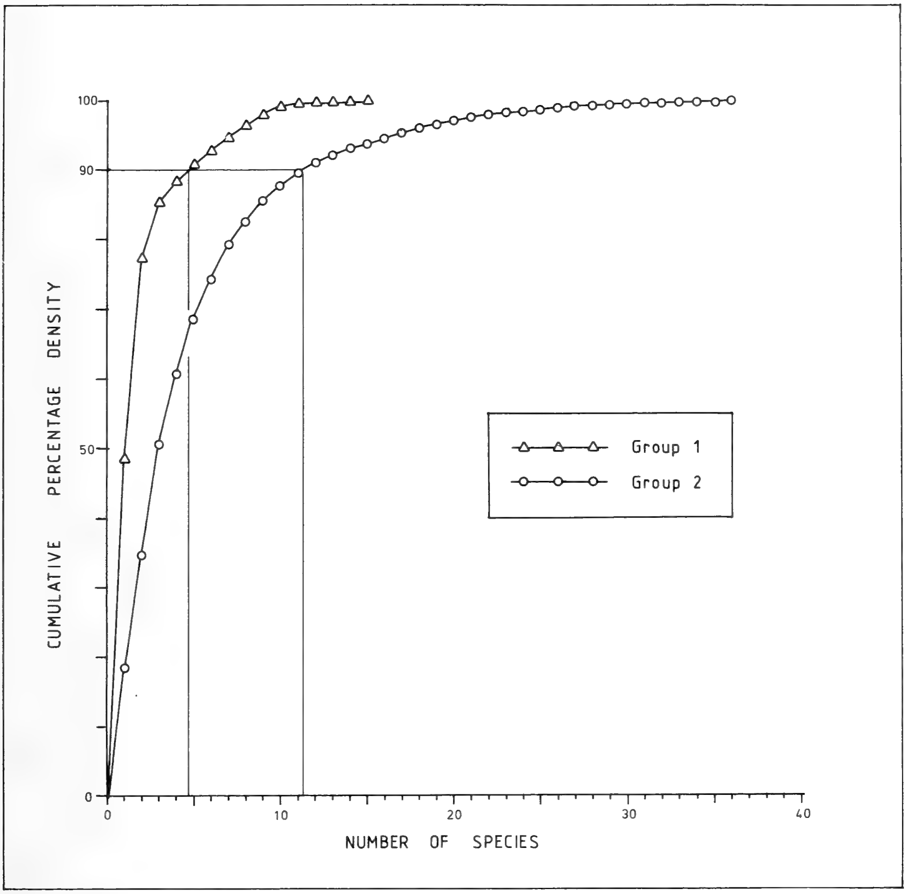

Fig. 14. Graph of cumulative percentage densities for Group 1 and Group 2.

Widespread Patterns, and 1 species (*Hygophum benoiti*) is said to have a North Temperate Pattern (Hulley 1981). Cumulative percentage density plots (Fig. 14) reveal that 11 species (with $2\triangle I_i > 6{,}63$) comprise about 90 per cent of the total, more than double the number in Group 1. Shannon diversity indices (H) for the stations range between 0,91 and 1,21 (Table 7). It should be noted that *Hygophum benoiti*, which has been included in the Temperate-subtropical Subpattern of the Cool Water Group (Hulley 1981), is a Group 2 indicator.

Only one species (*Lampanyctus cuprarius*, an Atlantic endemic) is characteristic of Group 3, when compared with Groups 1 and 2 (Table 6). It would appear therefore that the community structure of Group 3 is not different from that of Group 2 and that the distinction of these two groups is based rather on species abundances. This feature has already been noted (Backus *et al.* 1969) and is probably linked to differences in food supply, as indicated by the primary

TABLE 7

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Shannon Index of Diversity (H) and Evenness (J) based on 63 myctophid species. Maximum depth of haul in metres; computer station number in parenthesis, following AD station numbers.

Depths 0–210 m	Depths 211–350 m	Depths >1 800 m	Latitude
Group 1 (H_{max} = 1,79)			
		398/79 (38) H = 0,52 J = 0,29	48°N
390/79 (36) H = 0,47 J = 0,26	391/79 (37) H = 0,60 J = 0,33	389/79 (35) H = 0,81 J = 0,45	46°N
381/79 (33) H = 0,47 J = 0,26	382/79 (34) H = 0,64 J = 0,35	380/79 (32) H = 0,85 J = 0,47	45°N
372/79 (30) H = 0,54 J = 0,30	373/79 (31) H = 0,42 J = 0,24	371/79 (29) H = 0,61 J = 0,34	45°N
364/79 (27) H = 0,95 J = 0,53	365/79 (28) H = 0,77 J = 0,43	361/79 (26) H = 1,12 J = 0,62	42°N
Group 2 (H_{max} = 1,79)			
		348/79 (25) H = 1,16 J = 0,64	35°N
	346/79 (24) H = 0,94 J = 0,53	345/79 (23) H = 1,14 J = 0,64	35°N
339/79 (21) H = 1,09 J = 0,61	340/79 (22) H = 1,17 J = 0,65	338/79 (20) H = 1,07 J = 0,60	34°N
330/79 (18) H = 1,01 J = 0,56	331/79 (19) H = 1,21 J = 0,67	329/79 (17) H = 1,08 J = 0,60	33°N
322/79 (15) H = 0,94 J = 0,52	323/79 (16) H = 1,07 J = 0,59	321/79 (14) H = 1,12 J = 0,62	32°N
314/79 (12) H = 0,97 J = 0,54	315/79 (13) H = 1,05 J = 0,58		31°N
269/79 (2) H = 0,91 J = 0,51	270/79 (3) H = 0,93 J = 0,52		31°N
309/79 (10) H = 0,91 J = 0,51			30°N
Group 3 (H_{max} = 1,79)			
		268/79 (1) H = 1,07 J = 0,60	31°N
		314/79 (11) H = 0,86 J = 0,48	31°N
		308/79 (9) H = 0,76 J = 0,42	30°N
		276/79 (4) H = 0,94 J = 0,52	29°N
	302/79 (8) H = 0,97 J = 0,54	301/79 (7) H = 0,98 J = 0,55	28°N
		293/79 (6) H = 1,00 J = 0,56	26°N
		284/79 (5) H = 0,80 J = 0,45	26°N

productivity values of the two areas (Hela & Laevastu 1962). However, examination of our data and those of Nafpaktitis *et al.* (1977) reveals that the following species, present in Group 2, have never been recorded from the South Sargasso Sea Province: *Diaphus bertelseni, D. lucidus, Lampadena chavesi,* and *Notoscopelus bolini. Hygophum hygomii* occurs at seven of the eight MT–1600 stations of Group 3 and is represented in the IKMT data by a single specimen (SL 17 mm) from 27°51′N 52°11′W. Shannon diversity indices for Group 3 stations range between 0,76 and 1,07 (Table 7).

Table 8 lists the indicator species extracted from the IKMT data using information statistics. In general, there is good agreement between this set and the set obtained from our MT–1600 data (Tables 4–6). However, there are three exceptions (*Lampanyctus crocodilus, L. photonotus*, and *Notoscopelus bolini*). These, we feel, are a reflection of the limitations of the IKMT sampling method (see above) and should therefore be treated with extreme caution.

TABLE 8

1979–Sargasso Sea Expedition (2nd leg). IKMT hauls: Indicator species based on information statistic (*I*-) tests, where $2\triangle I_i > 6{,}63$. Anomalous species (marked with an asterisk) are discussed in the text.

Group 1	Group 2	Group 3
Benthosema glaciale	*Benthosema suborbitale*	* *Lampanyctus photonotus*
Ceratoscopelus maderensis	*Bolinichthys indicus*	
Myctophum punctatum	*Ceratoscopelus warmingii*	
Notoscopelus kroeyerii	*Diogenichthys atlanticus*	
	Hygophum hygomii	
	* *Lampanyctus crocodilus*	
	Lampanyctus pusillus	
	Lepidophanes gaussi	
	Lobianchia dofleini	
	Lobianchia gemellarii	
	* *Notoscopelus bolini*	
	Notoscopelus resplendens	

In summary then, the number of species comprising the myctophid community in Group 1 (North Atlantic Temperate Region) is less than the number in Groups 2 and 3 (North Atlantic Subtropical Region), with correspon-ding lower values for the index of diversity, but a greater degree of dominance among the most abundant species. The apparent increase in the species diversity index (H) with increasing depth (Table 7) is an artifact. The MT–1600, which is not an opening and closing net, samples the entire water column to the maximum fishing depth of a particular haul.

Because of this, detailed examination of the correlation between fishing depth and the subgroupings within each of Groups 1, 2, and 3 is somewhat presumptuous. Such discussion is further constrained by the variable nature of the sampling programme carried out during the transect. Firstly, two shallow hauls

and their associated deep haul were not made at each sampling position; except at a single station (AD 302-I/79), all Group 3 hauls were deep (Fig. 7); and only in the case of the Group 2 stations were shallow hauls (110–380 m) made at night and corresponding deep hauls (1 300–1 950 m) made during the day (Fig. 6). Secondly, shallow night hauls were aimed at just below or just above the deep scattering layer (DSL) read from echo-sounder traces; deep day hauls were fished either as deep as possible, the depth being determined from the depth-time recorder on completion of the haul, or to an arbitrary selected depth of about 2 000 m, dictated by the length of trawling warp deployed. However, in order to assess which species differ most between these subgroupings information statistic tests were performed on the relevant data. The results of the tests are presented in Tables 9, 10, and 11.

Table 9 lists the species that are characteristic of Groups 1A and 1B. No species occurs at all stations in one group and in none of the samples of the other group, although *Ceratoscopelus maderensis* and *Lampanyctus intricarius* approxi-

TABLE 9

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence (F) and numbers of individuals (N) of species, ranked according to information statistics, which distinguish Group 1A (F_{1A}, N_{1A}) from Group 1B (F_{1B}, N_{1B}). Asterisks (*) refer to Group 2 indicator species. Other conventions as in Table 4.

Species	F_{1A} (9)	N_{1A}	F_{1B} (4)	N_{1B}	$2\Delta I$
Group 1A					
Benthosema glaciale	9	11 439	4	259	6 537,369
Notoscopelus kroeyerii	9	7 062	3	101	4 370,428
Myctophum punctatum	8	1 940	4	29	1 192,920
Notoscopelus bolini	4	742	1	1	532,841
Ceratoscopelus maderensis	9	612	1	1	437,617
**Lampanyctus pusillus*	9	559	2	4	372,998
Symbolophorus veranyi	8	485	3	9	287,978
**Hygophum benoiti*	5	368	0	0	270,645
Diaphus rafinesquii	9	439	3	19	209,518
**Bolinichthys indicus*	4	255	1	1	176,811
Diaphus holti	8	376	3	18	172,701
Electrona risso	8	411	4	26	166,403
**Lobianchia dofleini*	3	192	0	0	141,206
**Lobianchia gemellarii*	8	238	4	32	53,931
**Hygophum hygomii*	3	66	0	0	48,540
**Lampanyctus ater*	5	58	1	2	29,833
**Lampanyctus photonotus*	4	32	0	0	23,534
Lampanyctus intricarius	8	51	2	4	18,267
Lampanyctus crocodilus	9	222	4	63	10,685
Diaphus metopoclampus	4	14	0	0	10,296
**Gonichthys cocco*	2	6	0	0	4,413
Group 1B					
Lampanyctus macdonaldi	0	0	3	14	33,002

mate this condition for Group 1A and *Lampanyctus macdonaldi* for Group 1B. In the main, differences in abundances are responsible for the high $2\triangle I_i$ values. Bearing in mind both the constraints pointed out above and the vertical distribution data given in the literature, it would appear either that day samples (*c*. 2 000 m) were below the depths of maximum abundance of the species and night samples (155–350 m) were targeted at depths of maximum abundance, or that the species are more dispersed vertically in the water column during the day than at night, or both. The first ten species, ranked according to their $2\triangle I_i$ values, have their maximum abundance in the upper 100 m at night. During the Mid-Atlantic Ridge cruise in June 1982, *Lampanyctus macdonaldi* was not taken at depths less than 870 m, while during the TIFI–8 cruise in May 1983, it was not taken at depths shallower than 600 m (ISH unpublished data), both of which would support the result in Table 9. Certain subtropical species (Group 2 indicators: *Bolinichthys indicus, Gonichthys cocco, Hygophum benoiti, Hygophum hygomii, Lampanyctus ater, Lampanyctus photonotus, Lampanyctus pusillus, Lobianchia dofleini*), which transgress the boundary zone into the Temperate Region, also serve to distinguish Group 1A from Group 1B. As is to be expected, they are either absent from the deeper (= colder; see Fig. 12) samples of Group 1B or occur in small numbers, perhaps representing contamination of the catch when the net is heaved through the overlying warmer water layers. The higher values for *Lobianchia gemellarii* in both Group 1A and Group 1B (Table 9) could be accounted for by the expatriate distribution pattern of this species in the temperate North Atlantic (Hulley 1981). *Gonichthys cocco*, a surface-migrating broadly tropical species, is not well sampled by the MT–1600 (p. 33), so that its inclusion in Table 9 should be treated with reservation.

Table 10 lists the species that serve to distinguish Group 2A (shallow night hauls: 110–380 m) from Group 2B (deep day hauls: 1 300–1 950 m). Again, no species occur in all samples of Group 2A and in none of Group 2B or vice versa. Higher abundance values at night are responsible for the two groupings. Only two temperate species (Group 1 indicators: *Diaphus holti, Notoscopelus bolini*) are included in Group 2A. As pointed out above, *Notoscopelus bolini* samples taken during the transect, south of the boundary between the Temperate and Subtropical Regions, are small juveniles (22–42 mm), while *Diaphus holti* was recorded only from the two stations immediately to the south of the boundary zone. Two species are characteristic of Group 2B: *Taaningichthys bathyphilus*, a bathypelagic widespread species, is known only from depths below 500 m; and *Electrona risso*, a Group 1 (Table 4) indicator species. The present analysis suggests that *Electrona risso* may occupy shallower depths in the Temperate Region than it does in the Subtropical Region.

The separation of Group 3A from Group 3B appears to be related to geographical position rather than to depth. One shallow haul only is included in Group 3 and the hauls of Group 3B represent the most southerly stations occupied during the transect. As pointed out above, differences between Group 2 and Group 3 stations rest primarily on the relative abundances of the species in

TABLE 10

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence (F) and numbers of individuals (N) of species, ranked according to information statistics, which distinguish Group 2A (F_{2A}, N_{2A}) from Group 2B (F_{2B}, N_{2B}). Asterisks (*) refer to Group 1 indicator species; dagger signs (†) refer to Group 3 indicator species. Other conventions as in Table 4.

Species	F_{2A} (12)	N_{2A}	F_{2B} (5)	N_{2B}	$2\triangle I$
Group 2A					
Lobianchia gemellarii	12	4 212	5	75	2 362,144
Hygophum hygomii	12	4 116	5	98	2 176,223
Ceratoscopelus warmingii	12	4 739	5	255	1 911,513
Hygophum benoiti	11	2 626	5	82	1 294,966
Lobianchia dofleini	11	2 122	5	44	1 155,918
Bolinichthys indicus	12	1 432	5	42	718,678
Diaphus mollis	12	1 299	4	28	701,953
Lampanyctus photonotus	12	781	4	9	467,639
Lampanyctus pusillus	12	831	5	32	383,549
Lepidophanes gaussi	11	442	3	5	265,266
Lampadena urophaos atlantica	9	369	2	2	237,064
Notoscopelus resplendens	12	584	5	41	204,540
Notoscopelus caudispinosus	12	318	4	13	143,692
Benthosema suborbitale	9	220	1	2	135,220
Lampadena chavesi	9	200	2	8	91,085
Hygophum reinhardtii	11	198	4	10	82,195
Lepidophanes guentheri	6	140	2	2	81,399
Diaphus effulgens	7	139	1	3	75,092
Taaningichthys minimus	9	147	3	6	66,462
**Notoscopelus bolini*	5	176	3	11	65,856
Lampanyctus festivus	11	168	3	10	64,495
Diaphus splendidus	6	60	0	0	41,797
Diaphus brachycephalus	6	71	1	1	41,368
Hygophum taaningi	2	48	0	0	33,437
Diaphus lucidus	7	61	1	3	25,617
Diaphus problematicus	3	32	0	0	22,292
Diaphus perspicillatus	3	31	0	0	21,595
**Diaphus holti*	1	43	1	2	19,092
Myctophum selenops	6	43	1	2	18,486
Notolychnus valdiviae	3	26	0	0	18,112
Lampanyctus ater	8	186	5	41	15,483
Diaphus dumerilii	4	21	0	0	14,629
†*Lampanyctus cuprarius*	8	106	5	20	12,527
Group 2B					
Taaningichthys bathyphilus	0	0	3	10	24,476
**Electrona risso*	1	8	2	13	9,481

the two groups. This can be linked to differences in food supply, as indicated by primary productivity values for the two geographic areas. The inclusion of a single species, *Hygophum taaningi* (Broadly Tropical Pattern: Thermophilic Eurytropical Subpattern), in Group 3B (Table 11) would tend to support this hypothesis, since the species has a comparatively shallow night distribution between the surface and 250 m.

TABLE 11

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence (F) and numbers of individuals (N) of species, ranked according to information statistics, which distinguish Group 3A (F_{3A}, N_{3A}) from Group 3B (F_{3B}, N_{3B}). Asterisks (*) refer to Group 2 indicator species. Other conventions as in Table 4.

Species	F_{3A} (5)	N_{3A}	F_{3B} (3)	N_{3B}	$2\triangle I$
Group 3A					
**Lobianchia gemellarii*	5	152	3	6	103,632
Lampanyctus cuprarius	5	170	3	14	88,233
**Ceratoscopelus warmingii*	5	141	3	14	65,986
**Hygophum hygomii*	5	65	2	3	42,394
**Diaphus mollis*	5	54	1	2	37,427
**Lepidophanes gaussi*	4	37	0	0	34,780
**Hygophum reinhardtii*	4	16	0	0	15,040
**Notoscopelus resplendens*	1	13	0	0	12,220
**Lampanyctus photonotus*	4	47	3	11	9,415
**Myctophum selenops*	2	9	0	0	8,460
**Bolinichthys indicus*	4	30	3	6	7,530
**Lampanyctus lineatus*	4	13	1	1	6,977
....					
**Notoscopelus caudispinosus*	3	16	2	2	6,405
**Lobianchia dofleini*	2	6	0	0	5,640
Group 3B					
....					
**Hygophum taaningi*	1	4	3	10	6,625

Inverse ('r'-type) analysis

The grouping of the species with inverse (or 'r'-type) analysis was only partially successful in revealing distribution pattern types. Initially all 63 species from the MT–1600 transect were included, but this led to a somewhat complex dendrogram (Fig. 15), with many species showing little similarity to others. These are either rare species, or species that are poorly represented in the R.V. *Anton Dohrn* catches. These species were then excluded from the analysis by the criterion of occurring at fewer than 10 stations and in densities of less than 6 specimens per hour per station of occurrence, as shown in Figure 16. The reduced data matrix was then reworked through the programme. The resulting dendrogram (Fig. 17) is somewhat clearer, indicating the existence of two major species groups: those found in the Temperate Region; and those found in the Subtropical Region and South Sargasso Sea Province. A similar picture of these two groupings was obtained from the IKMT data. Unfortunately, neither the dendrograms nor the ordinations allow for the recognition of the various distribution-pattern types that have been formulated in the literature. We suggest that this may be due to the fact that only the southern ranges of the temperate species and the northern ranges of the tropical and subtropical species were covered by the transects.

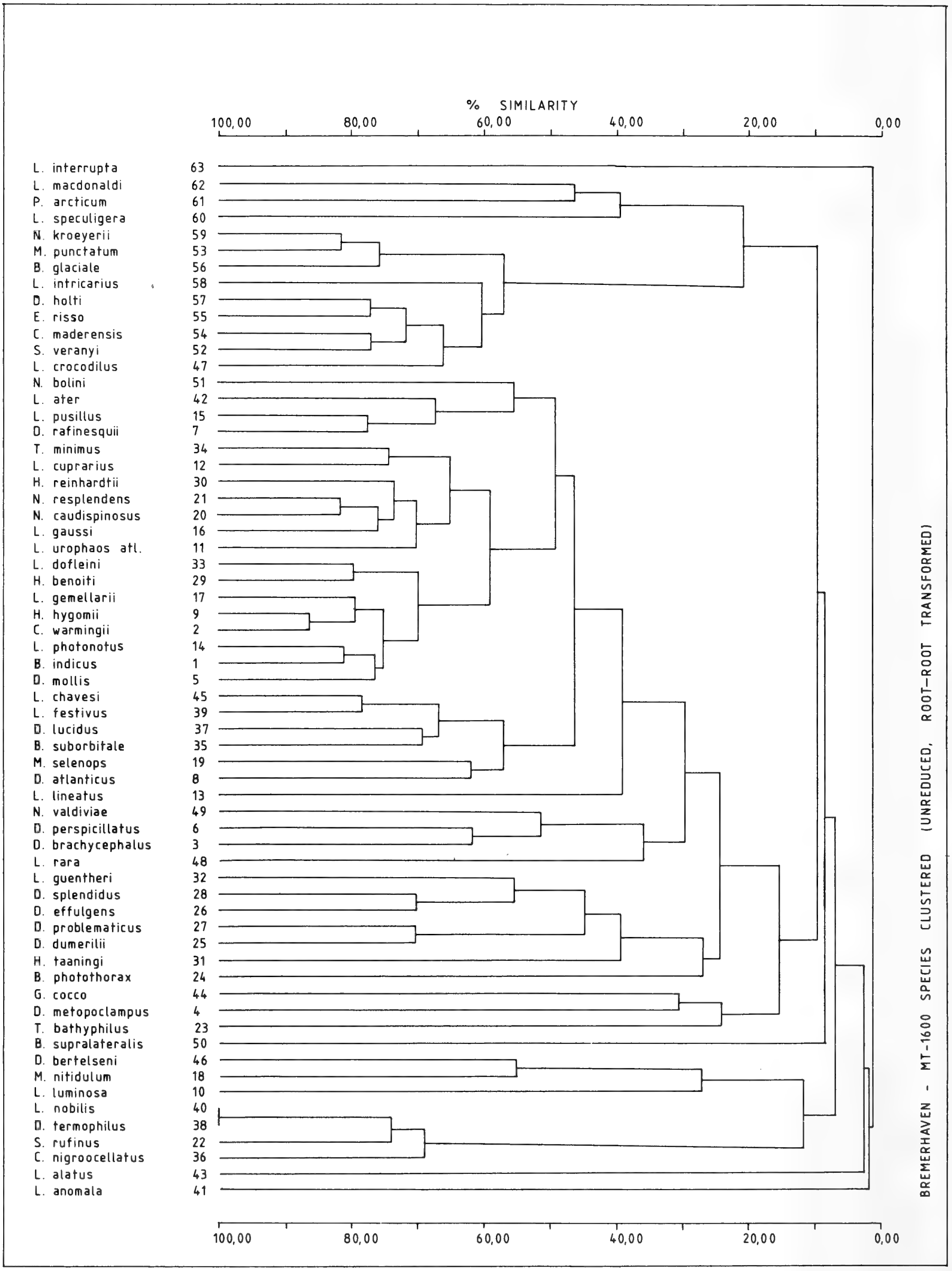

Fig. 15. Dendrogram of species affinities for 63 species from MT-1600 hauls.

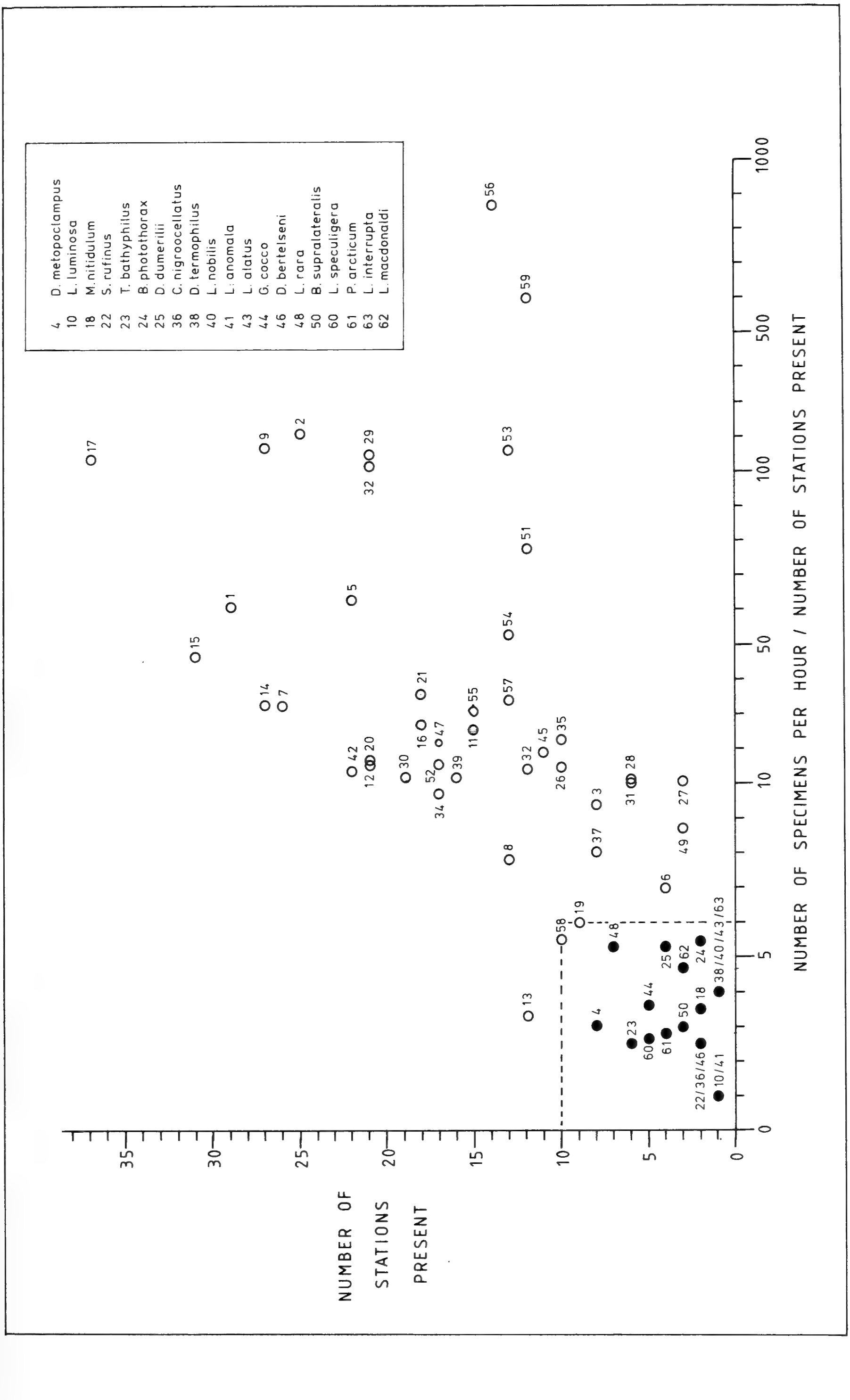

Fig. 16. Graph of the station occurrences and densities of myctophids from MT–1600 hauls. Solid circles—those species excluded from further analysis.

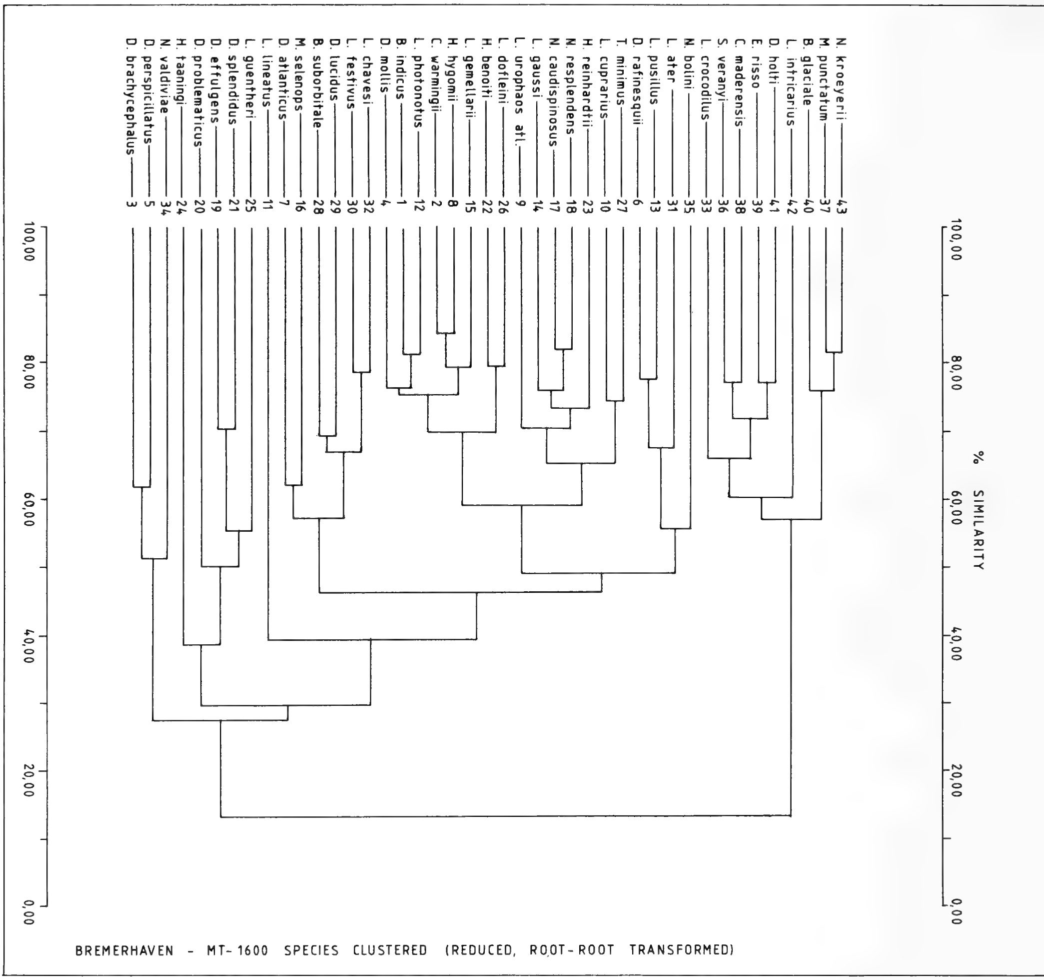

Fig. 17. Dendrogram of species affinities for reduced number of species from MT–1600 hauls.

In discussing the second and third aims of this paper (see p. 20), the distributions of *Hygophum benoiti* (characteristic of the subtropical grouping) and *Electrona risso, Benthosema glaciale*, and *Lampanyctus crocodilus* (all characteristic of the Temperate Region) are examined.

Backus *et al.* (1977) are of the opinion that *Electrona risso* (Fig. 18) is an Eastern Pattern species, which would seem to support its inclusion with the other temperate species in the context of the 1979–transects. Hulley (1981), on the other hand, suggests a relationship with the 10 °C and 15 °C isotherms at 200 m and the 50 $gCm^{-2}y^{-1}$ isoline. Except for the single larval specimen taken in a neuston tow at about 28°N 51°W, for which there is some doubt about the identification (H.-C. John, pers. comm.), the latter criteria are satisfied by the

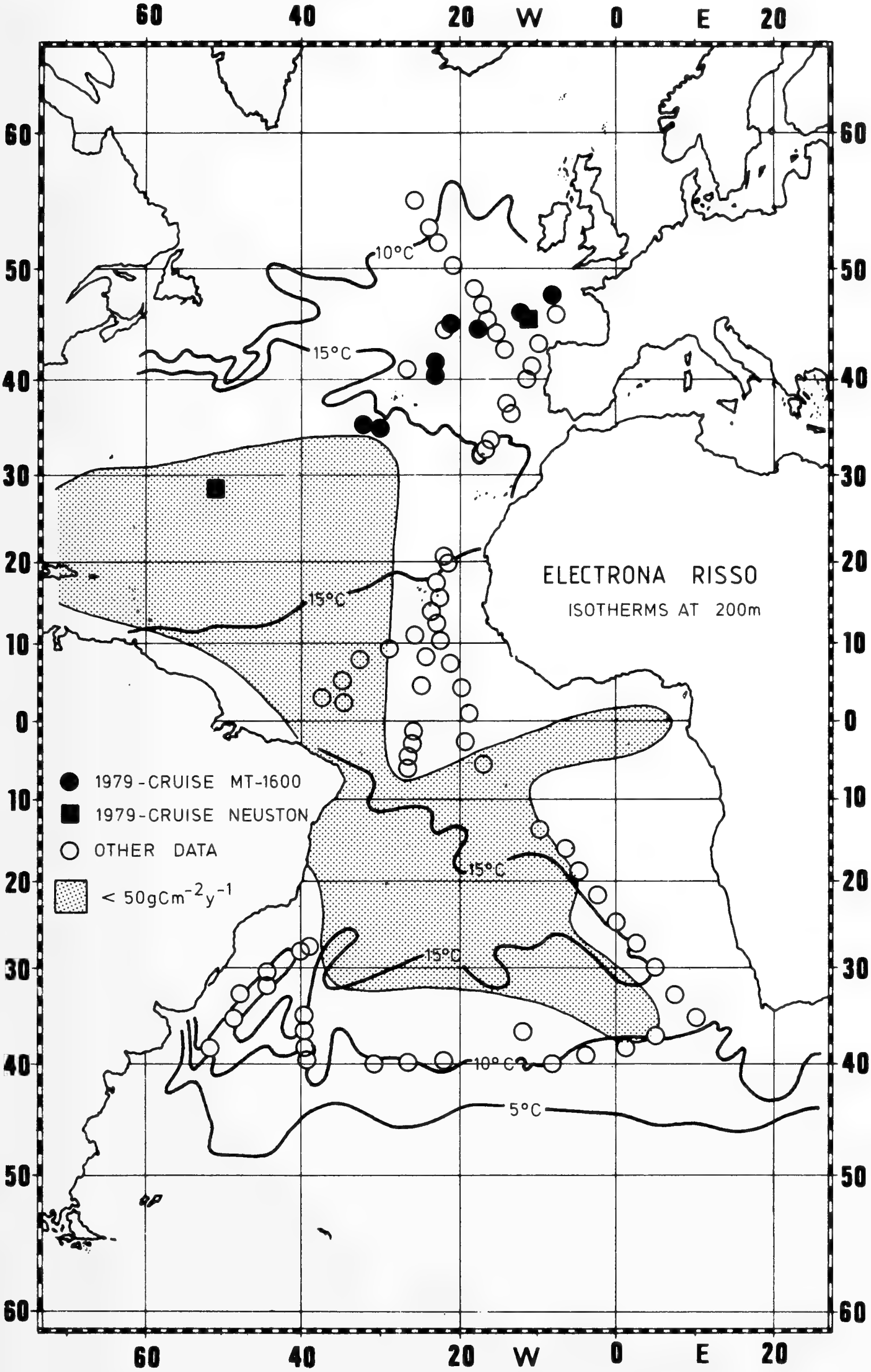

Fig. 18. Distribution of *Electrona risso*.

1979–transect data. Seen against a background of an extensive distribution, particularly in the South Atlantic (Fig. 18), *Electrona risso* should be excluded from the Eastern Pattern and be considered a widespread species within the apparent ecological constraints.

Hygophum benoiti has been described as a temperate-semisubtropical species by Backus *et al.* (1977), and as a temperate-subtropical species, but within the Northern Temperate Pattern, by Hulley (1981). The present transect data and indicator analyses suggest that, while *Hygophum benoiti* is indeed distributed in both temperate and subtropical regions (Fig. 19) and attains sexual maturity throughout its distributional range, it shows a closer affinity to the Subtropical

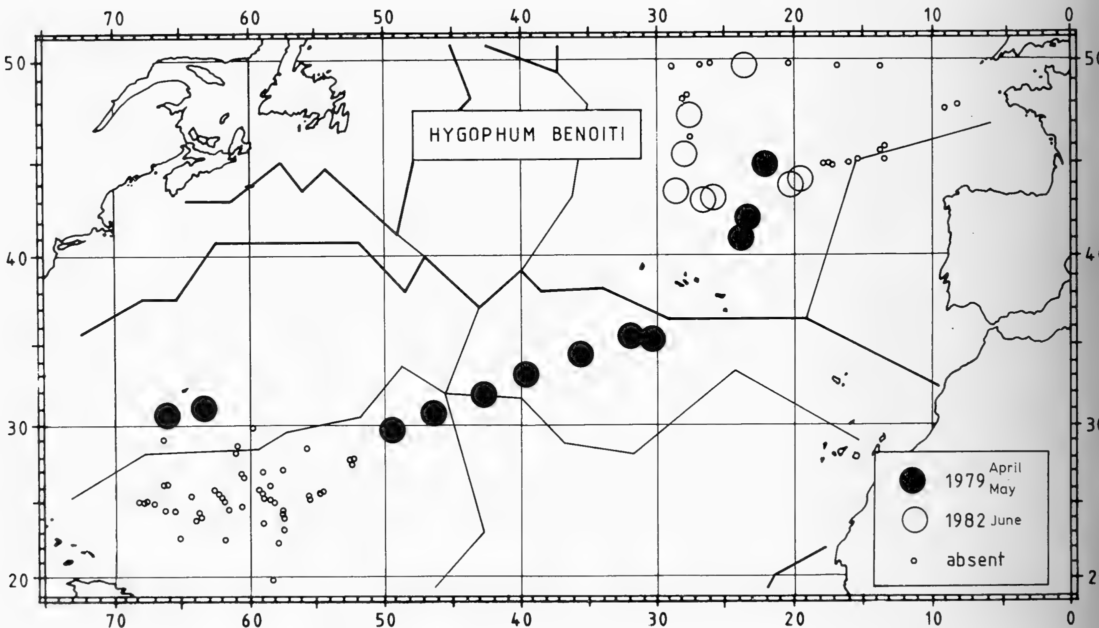

Fig. 19. Distribution of *Hygophum benoiti*.

Region than to the Temperate Region (Table 5). This suggestion was recently confirmed during the 1982–Mid-Atlantic Ridge Expedition, north of the Azores, where the species was taken in any quantity only south of about 44°S (unpublished data). This means that the distribution pattern of *H. benoiti* may be different from those of other species presently included in the Temprate-subtropical Pattern, namely *Ceratoscopelus maderensis, Diaphus rafinesquii, Notoscopelus bolini,* and *Symbolophorus veranyi.* This warrants a closer examination both of the above-mentioned temperate-subtropical species, and the species currently held under the North Subtropical Subpattern, e.g. *Lampadena urophaos atlantica*.

The distribution of *Benthosema glaciale* (Fig. 20), a shallow-living species with a night distribution between 12 m and 200 m, reveals that this Temperate Region indicator species transgresses the boundary limit, with a single specimen being taken in the northern Subtropical Region. Ordination of the MT–1600 data

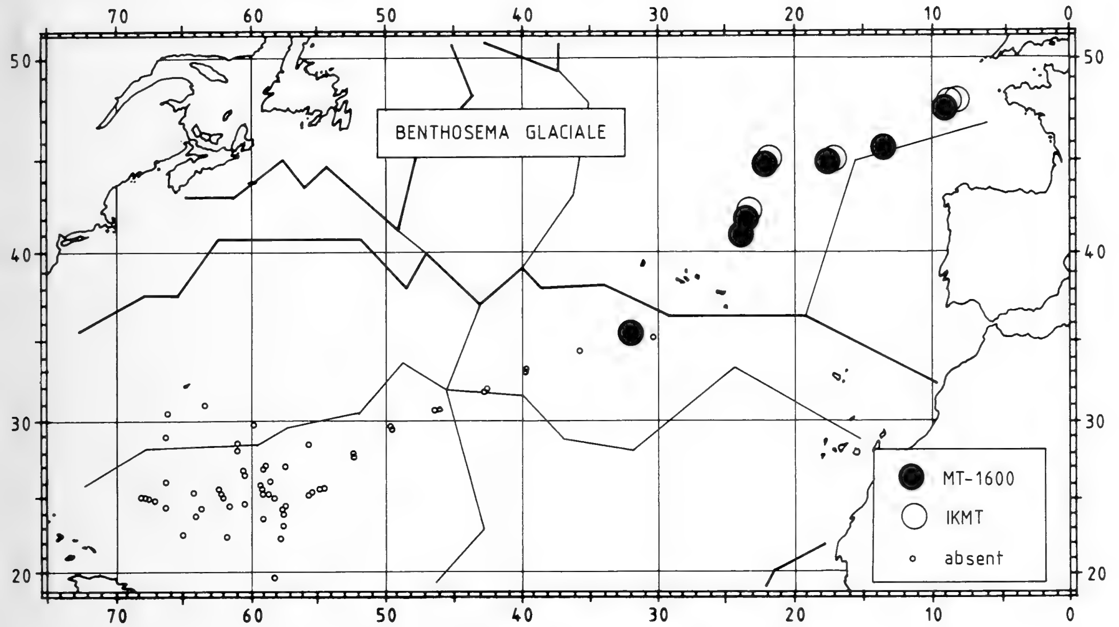

Fig. 20. Distribution of *Benthosema glaciale*.

for this species (Fig. 21) indicates that it was taken at all temperate stations, and further, that in this region there was no apparent size stratification with depth (although opening and closing nets were not employed). The specimen from the Subtropical Region is very small by comparison (Fig. 21) and may only indicate transportation of juveniles across the boundary by ocean currents. These juveniles may have no potential for achieving sexual maturity.

By contrast, *Lampanyctus crocodilus*, a somewhat deeper-living Temperate Region species, is also found to the south of the boundary between the Temperate Region and the Subtropical Region. In IKMT samples, it was taken to as far south as about 32°N, but only as small specimens (maximum SL 23 mm). The ordination (Fig. 22) reveals a marked size stratification with depth in the Temperate Region, and further, that large specimens do occur in deeper waters south of the Temperate Region boundary, to about 34°N. Since these specimens are of a potentially reproductive size (maximum SL 178 mm), future study will include the examination of changes in sexual maturity across this boundary zone.

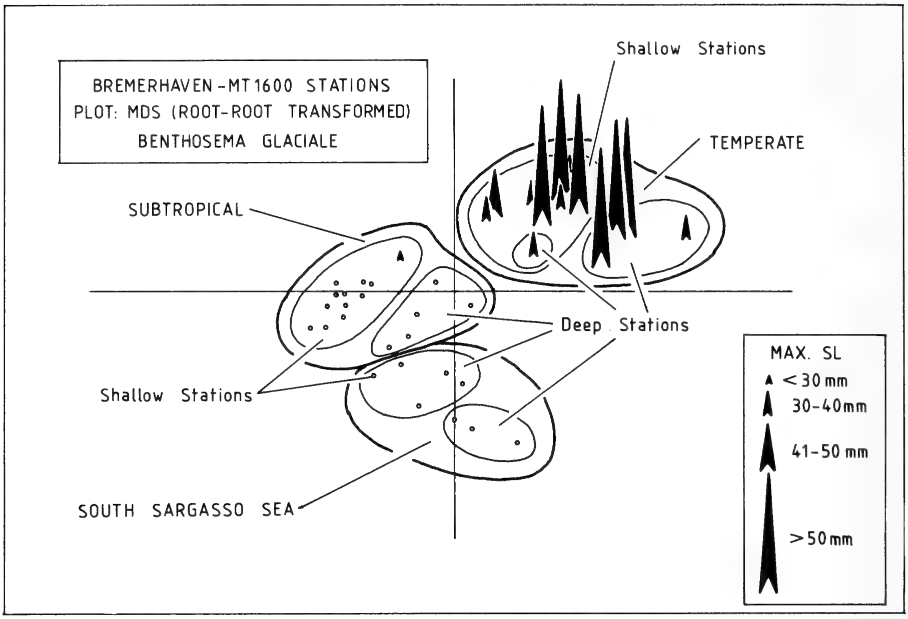

Fig. 21. MDS plot for *Benthosema glaciale* with maximum size indicated for each positive sample.

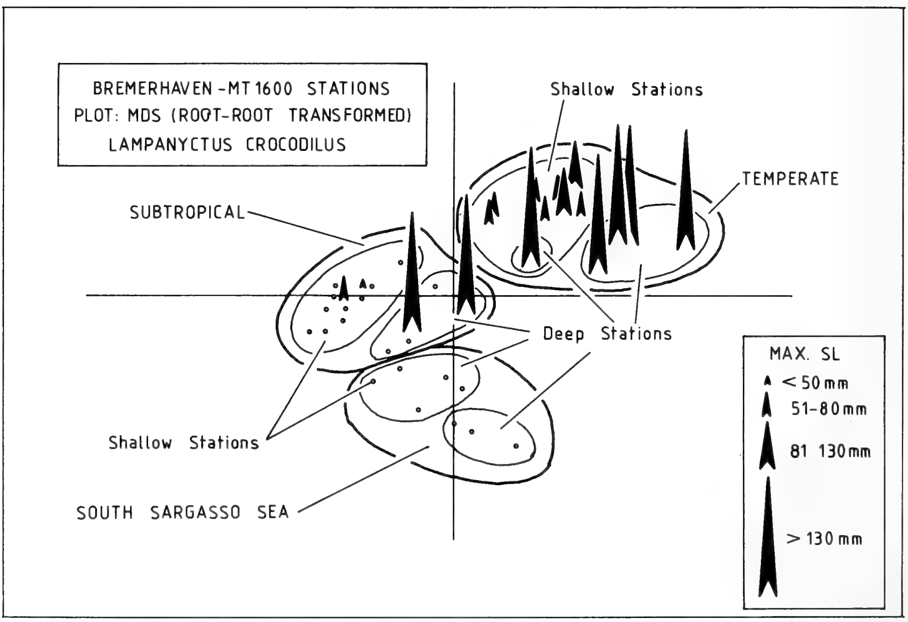

Fig. 22. MDS plot for *Lampanyctus crocodilus* with maximum size indicated for each positive sample.

A summary of the myctophid catch data from the MT–1600 transect is compared in Table 12 with the distributional patterns and subpatterns given by Hulley (1981, table 3). For a given pattern or subpattern, abundances have been calculated in mean number of specimens per hour for stations within each of the Groups 1, 2 and 3, according to the formula:

$$\text{Pattern}_j: \text{Abundance} = \frac{\sum\limits_{i(j)} \left(\sum\limits_{s(t)} n_{is} \right)}{\text{No. stations in } t}$$

where:

n_{is} is the number of specimens of species 'i' caught per hour at station 's';
j is the assembly of species within a particular distribution pattern;
t is the stratum of stations in each of Groups 1, 2 and 3.

However, some reservation is expressed with regard to the absolute values obtained with this gear, because of errors introduced while picking the net on deck, uncertainty of the exact time-span in which the net is actively fishing, and/or variations in the size of the mouth opening of the net.

No bathypelagic species of myctophid is endemic to the Atlantic. In the Warm Water Group of 42 species, 6 (14,3 %) are endemic to the Atlantic, while 11 (73,3 %) of the Cold Water Group of 15 species are endemic. Further, all myctophid species held under the North Temperate Pattern (Boreoarctic, Boreal, Mediterranean and Temperate-subtropical Subpatterns) in the Atlantic are endemic.

The Warm Water Group, representing 66,7 per cent of the total number of species, averaged 98 specimens per hour per station in Group 1 stations, 1 284 specimens per hour per station in Group 2 stations and 112 specimens per hour per station in Group 3 stations. Cold Water Group species, representing 23,8 per cent of the total number of species, averaged 1 862 specimens per hour per station in Group 1 stations, 202 specimens per hour per station in Group 2 stations and less than one specimen per hour per station in Group 3 stations. Widespread species, representing 6,3 per cent of the total number of species, averaged 48 specimens per hour per station, 136 specimens per hour per station, and one specimen per hour per station in Group 1, Group 2, and Group 3 stations respectively. Bathypelagic species, representing 1,6 per cent of the total number of species, averaged less than one specimen per hour per station in Group 2 and Group 3 stations and were absent in Group 1 stations.

The above confirms the general rule that species diversity decreases with increasing latitude and that larger populations occur in cold-water species than in warm-water species. Summed mean abundance values for stations in each of Groups 1, 2 and 3 give a measure of the 'standing stock' of the three areas: Group 1 (Azores–Britain Province) is 18 times more productive than Group 3 (South Sargasso Sea Province), while Group 2 (North Sargasso Sea Province–North North African Sea Province) is 14 times more productive than Group 3. In terms of oceanic myctophids, therefore, the North Atlantic Temperate Region is

TABLE 12

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Comparison of myctophid specimen abundances with distributional patterns and subpatterns as given by Hulley (1981).

	No. of species	*Percentage total no. of species*	*Group 1: mean no. specimens/hour*	*Group 2: mean no. specimens/hour*	*Group 3: mean no. specimens/hour*
MESOPELAGIC					
WIDESPREAD GROUP	4	6,3	48,38	136,12	0,88
Widespread Pattern	4	6,3	48,38	136,12	0,88
WARM-WATER GROUP	42	66,7	98,46	1 284,18	111,76
Tropical Pattern	7	11,1	0,31	12,65	2,75
Eurytropical Pattern	22	34,9	23,77	776,53	64,88
Subtropical Pattern	13	20,6	74,38	495,00	44,13
COLD-WATER GROUP	15	23,8	1 862,09	202,24	0,38
Bitemperate Pattern	4	6,3	6,46	0,00	0,00
Boreoarctic Subpattern	3	4,8	1 451,62	0,24	0,00
Boreal Subpattern	2	3,2	167,85	0,82	0,00
Mediterranean Subpattern	1	1,6	30,31	2,71	0,00
Temperate-subtropical Subpattern	5	7,9	205,85	198,47	0,38
BATHYPELAGIC					
WIDESPREAD GROUP	1	1,6	0,00	0,59	0,63
Widespread Pattern	1	1,6	0,00	0,59	0,63
WARM-WATER GROUP	1	1,6	0,00	0,00	0,13
Eurytropical Pattern	1	1,6	0,00	0,00	0,13
STANDING STOCK					
Summed mean abundance			2 008,93	1 623,13	113,78
Percentage			53,63	43,33	3,04

1,24 times more productive than the North Atlantic Subtropical Region. Recent unpublished data from the TIFI–8 Cruise, obtained while sampling a few metres above the slope regions west of Great Britain, indicate that this value would be considerably higher if the pseudoceanic population of *Notoscopelus kroeyerii* were to be included.

ACKNOWLEDGEMENTS

We would like to express our sincere thanks to Professor John Field and Mss Elaine Rumback and Patti Wickens of the Zoology Department, University of Cape Town, for setting up the data for the computer programme and for ensuing discussion and to Dr Doug Butterworth, Department of Applied Mathematics, University of Cape Town, for assistance with the estimation of abundances. We would also like to thank both the Captain and crew of the R.V. *Anton Dohrn* for collection of the material used in our analyses, and our colleagues on board, for rewarding discussions of the implications of distribution. A portion of this paper was originally presented at the Fourth Congress of European Ichthyologists. We thank the Fisheries Development Corporation (South Africa), the C.S.I.R. (Research Grants Division), and the Trustees of the South African Museum for funding travel expenses for the senior author to participate in the cruise and attend the Congress.

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An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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(a) The Figures, Maps and Tables of the paper when referred to in the text
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Punctuation should be loose, omitting all not strictly necessary

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Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

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P. ALEXANDER HULLEY & GERHARD KREFFT

A ZOOGEOGRAPHIC ANALYSIS OF THE FISHES OF THE FAMILY MYCTOPHIDAE (OSTEICHTHYES, MYCTOPHIFORMES) FROM THE 1979–SARGASSO SEA EXPEDITION OF R.V. *ANTON DOHRN*

8

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LATE HOLOCENE USE OF PENGUIN SKINS: EVIDENCE FROM A COASTAL SHELL MIDDEN AT STEENBRAS BAY, LÜDERITZ PENINSULA, SOUTH WEST AFRICA–NAMIBIA

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GRAHAM AVERY

South African Museum, Cape Town

(With 6 figures)

[*MS accepted 20 August 1984*]

ABSTRACT

Cut-marks on jackass penguin *Spheniscus demersus* humeri and tibiotarsi from a shell midden dated to 2000 BP are examined. Evidence from experimentation and the ethnographic record shows that the marks were produced while skinning the penguins. High frequencies of small convex scrapers and backed bladelets and segments are correlated with skinning and the preparation of penguin pelts. This is amongst the earliest evidence for the manufacture of skin garments in southern Africa.

CONTENTS

INTRODUCTION

This paper reports on unusual bones from samples excavated in 1972 and 1982 by W. E. Wendt from a shallow shell midden (maximum 0,3 m in depth, 50 m^2 in area, 12 m^3 in volume) at Steenbras Bay, Lüderitz Peninsula (26°40′S 15°07′E) (Fig. 1).* The 1972 excavation at the site of a trench 3,5 m^2 in area was reported on briefly by Wendt (1974). Material from the recent bulk sample is being processed. Radiocarbon dates are available: Pta 1049 (S3) 2070 ± 50 BP (charcoal) 10–20 cm; Pta 1045 (S2) 2540 ± 50 BP (limpet shell, *Patella* sp.) 20 cm; Pta 1042 (S1) 2440 ± 50 BP (limpet shell, *Patella* sp.) 3–5 cm (= surface). Vogel & Visser (1981) in reporting these dates state that the determinations run on the shells appear to be *c.* 420 years too old and that dating of the occurrence is, therefore, consistently at about 2000 BP.

* Wendt's collection will be deposited in the State Museum, Windhoek.

Ann. S. Afr. Mus. **96** (3), 1985: 55–65, 6 figs.

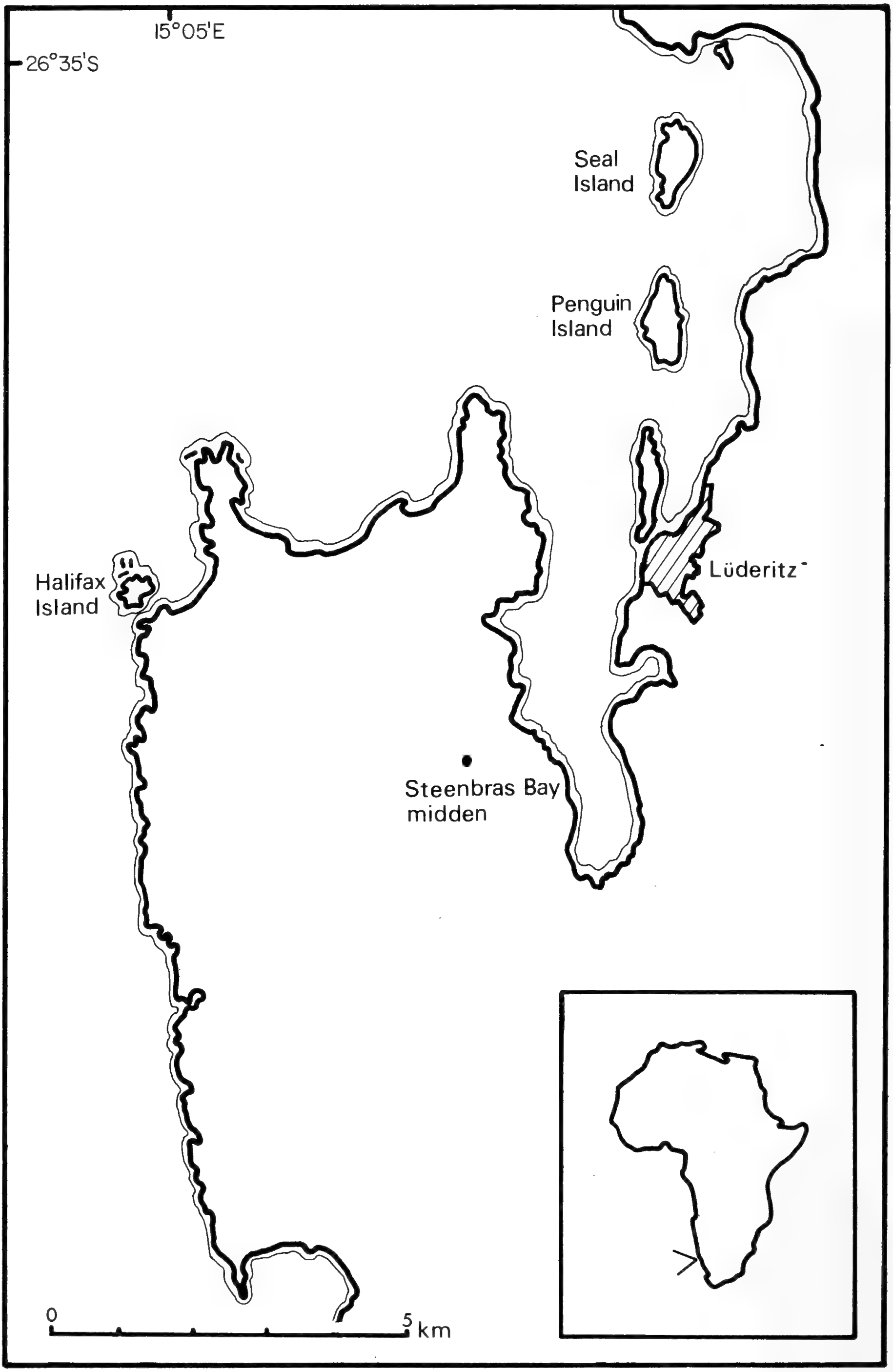

Fig. 1. Locality of Steenbras Bay midden and nearby islands.

PENGUIN BONES

Among the bones there is a series of jackass penguin (*Spheniscus demersus*) humeri and tibiotarsi bearing a series of obvious cut-marks (Fig. 2). Although other body parts were present in small numbers, no other evidence of cutting was found.

Humeri

The collection consists of two virtually complete left humeri (Fig. 2A, B), a proximal end of a left humerus (Fig. 2C), a shaft and distal fragment of a left humerus (Fig. 2D), and a shaft of a right humerus (Fig. 2E), representing a minimum of three individuals. All the bones are incompletely ossified and therefore of immature birds. Figure 2 shows that the cut-marks occur consistently on the proximal halves of the humeri.

Cut-marks are located in the capital groove and extend on to the head and bicipital surface. Others are on the median crest of the pneumatic fossa, deltoid crest, and the region of the nutrient foramen and attachment of the latissimus dorsi posterioris. The marks clearly resulted from cutting in the region where the flipper was attached to the body. The nature of the cut-marks and their extension towards the shaft suggest both that some form of sawing action was exercised and that the intention was to cut around the skin in order to remove it at the point where the paddle-like flipper joins the body. The logical goal, therefore, seems to have been to skin the bird. It would otherwise have been simple to rip off the skin, locate the joint and sever the attachments with little or no damage to the bone.

Tibiotarsi

A complete right tibiotarsus and a right distal end of a tibiotarsus of immature birds showed cut-marks on the distal shaft (Fig. 2F–G). Cutting was not as distinct as on the humeri. The position of the cut-marks, however, corresponds to the point at which feathered skin on the leg becomes the bare skin of the foot. This too is consistent with the suggestion that the marks resulted from skinning the birds.

STONE ARTEFACTS

It is postulated that the relatively high frequencies of small convex scrapers and backed bladelets (Fig. 3) that occur in the Steenbras Bay stone assemblage may be correlated with skinning activities and the preparation of pelts, perhaps not only of penguins but also of other animals such as the Cape fur seal *Arctocephalus pusillus*. Recent examinations of the function of small convex scrapers (Deacon & Deacon 1980; Binneman 1984) support the suggestion that they were used hafted as skin scrapers. Only a limited number of backed bladelets and segments have been examined as yet but Binneman (1984) has suggested that

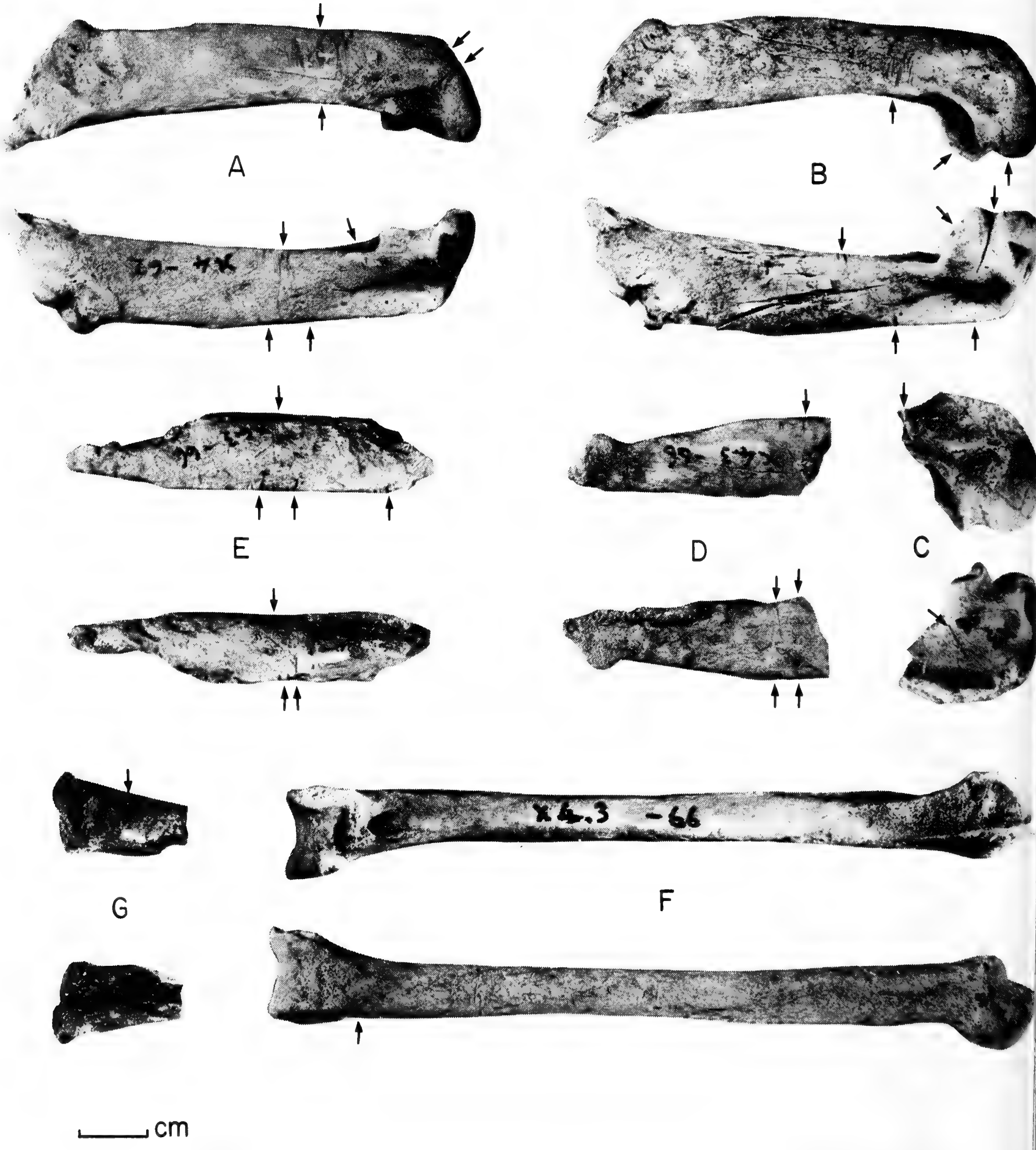

Fig. 2. Jackass penguin bones from Steenbras Bay midden (collected by W. E. Wendt). A–E. Humeri. F–G. Tibiotarsi. Arrows indicate location of cut-marks. Note sinuous lines caused by rootlets.

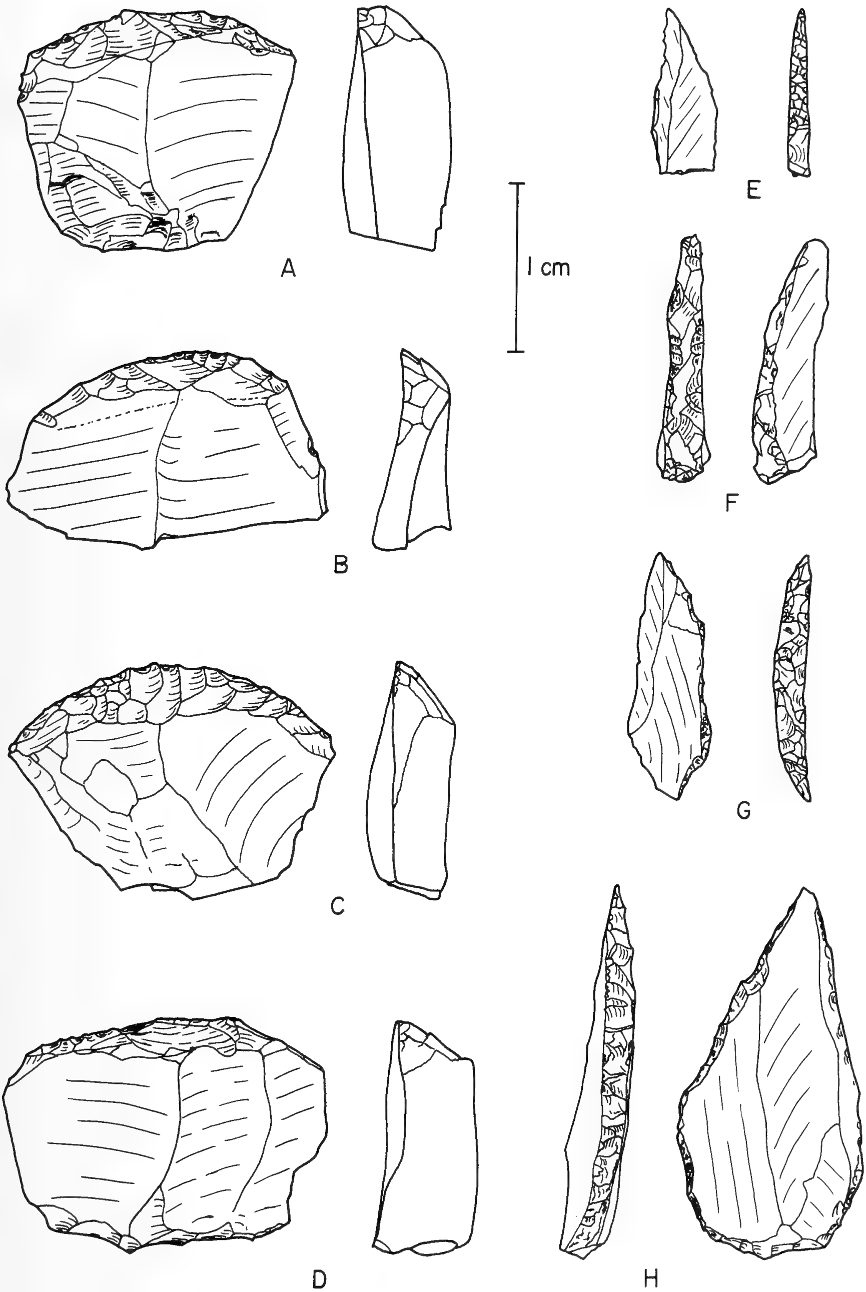

Fig. 3. Examples of some stone artefact types from the Steenbras Bay midden (collected by W. E. Wendt). A–D. Small convex scrapers (raw material: cryptocrystalline silica); broken line near worked edge of B indicates edge of mastic trace. E–H. Backed blades (raw material: quartz).

they were hafted in series for cutting in much the same manner as a penknife. It seems reasonable, therefore, to assume that the occurrence in relatively high frequencies of convex scrapers and backed bladelets together with evidence pointing to skinning is not fortuitous.

SKINNING EXPERIMENT

Experimental skinning of adult and immature penguins killed in an underwater explosion and an oil spill confirmed that the archaeological cut-marks could have been produced in the manner suggested above (Fig. 4). It proved difficult to remove the skin by cutting at the body–flipper link using decisive cuts. This was because displaced feathers formed a mat under the blade preventing penetration. Furthermore, the skin itself was loose over the bone necessitating a number of cuts before it was completely detached. It was noted that careful skinning at this point and at the tibiotarsus (thereby leaving the smallest possible holes in the pelt requiring closing), and under the tail at the vent made the most economical use of the whole skin. The pelt produced from the juvenile specimen (Fig. 5) was in the form of a dark oval centre bordered by white. In the case of a bird in adult plumage the dark centre is bordered by white with a black stripe (Brown *et al.* 1982).

After the bird was skinned the skeleton was prepared. Cut-marks produced around the proximal end of the humerus during skinning were found in the same position as the marks on the Steenbras Bay specimens (Figs 2, 4). They did, however, differ in their morphology. The most likely explanation for this is that a steel-bladed knife was used in the experiment whereas a stone-bladed tool was probably used on the specimens from Steenbras Bay. Similar cut-marks were produced on the distal region of the tibiotarsus where the skin was removed from the hind limbs of the penguin (Figs 2, 4).

ETHNOGRAPHIC EVIDENCE FOR THE USE OF PENGUIN SKINS

At least two lines of ethnographic evidence suggest that penguin skins were used in the making of garments. Owen (1833: 229) described indigenous people at Walvis Bay as being '. . . clothed in skins of either beasts or penguins, which being in an undressed state, constituted a centre of attraction for flies . . .'. A vignette drawn by Col. R. J. Gordon (Fig. 6) depicts a Nama group seen on the coast north of the Orange River in 1779. While some individuals are depicted wearing plain skin karosses, two are covered by completely different garments. These are apparently made of a number of pelts, each of which appears as a roughly oval dark form surrounded by a lighter colour. No mammal would produce pelts of this size and description and it is thought that they represent penguin pelts. This is supported both by the size, shape and number of the pelts, and details of texture depicted on both the external and internal surfaces (feather texture, and stippled internal texture created by feather roots). The detail

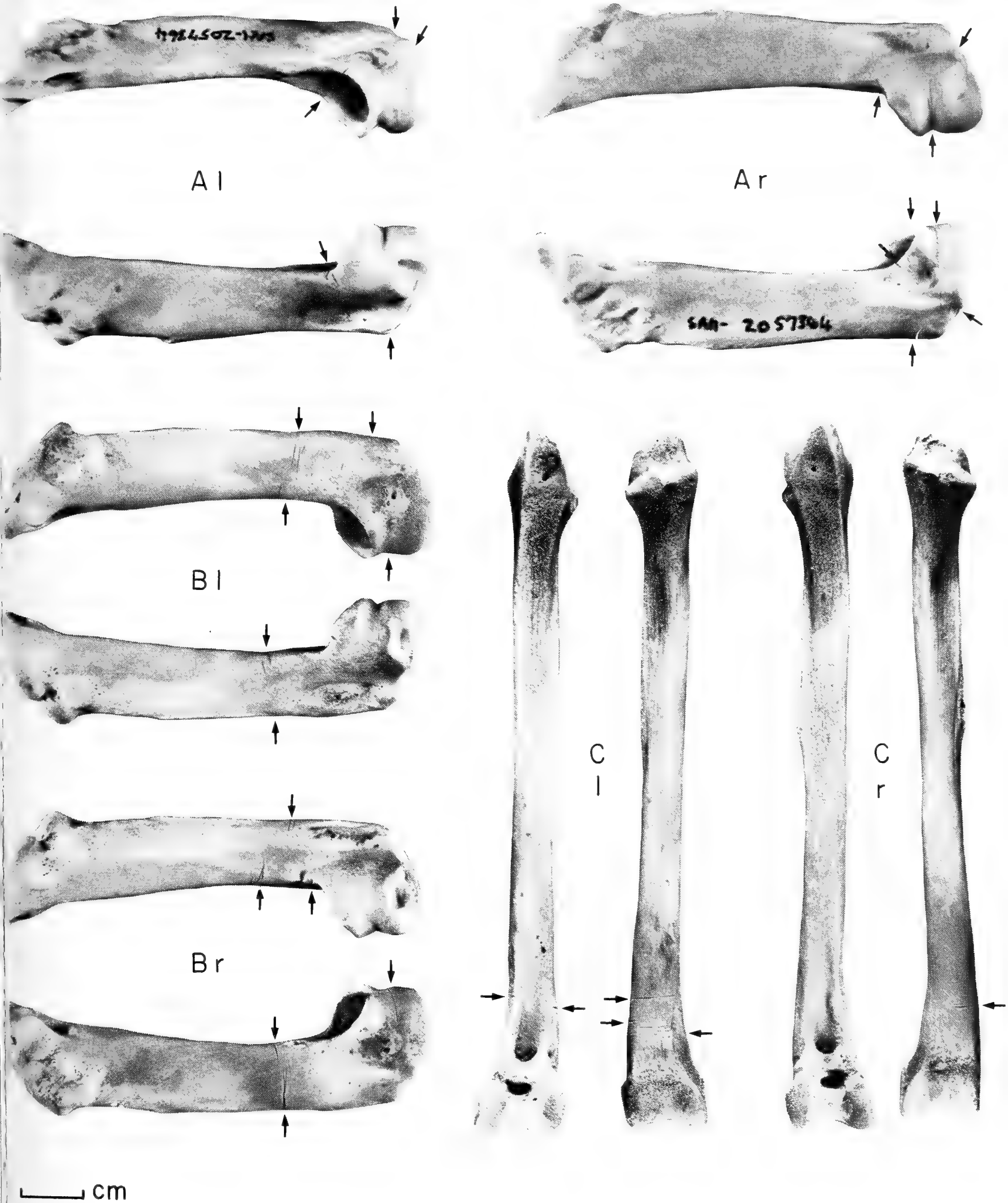

Fig. 4. Jackass penguin bones from experimental specimens. A. Humerus (SAM–ZO57364). B. Humerus (juvenile) (SAM–ZO57365). C. Tibiotarsus (juvenile) (SAM–ZO57365). Arrows indicate location of cut-marks; l = left, r = right.

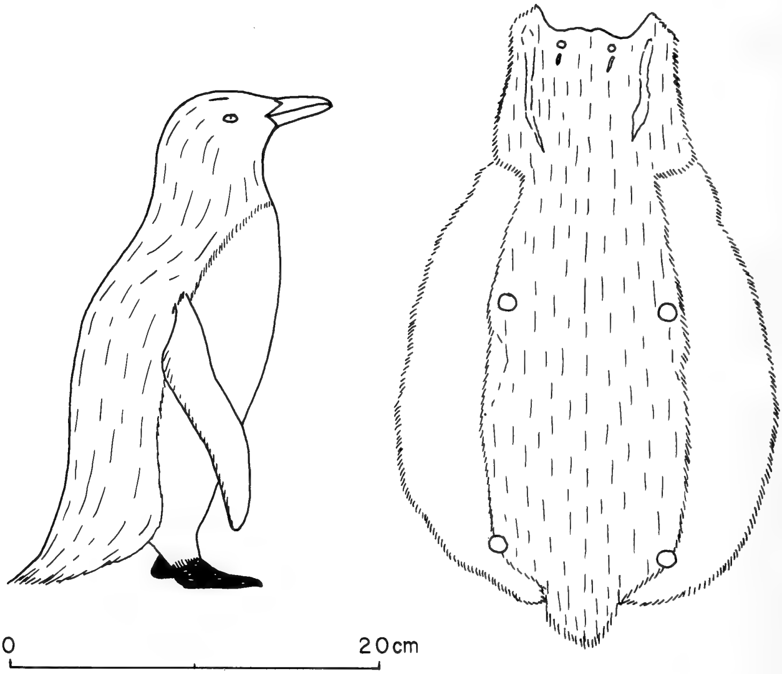

Fig. 5. A. Juvenile jackass penguin showing distribution of black and white feathering. B. Pelt from juvenile specimen, SAM–ZO57365. Note distribution of black and white areas and points (indicated by circles) at which humeri and tibiotarsi were removed. The holes are only visible from the ventral surface of the skin.

depicted, both as regards the karosses and as regards other aspects of activity, clothing, equipment, etc., suggests that Gordon was a keen observer of detail and that the depictions are accurate, in spite of a slight discrepancy where the black is not shown to extend down to the tail.

The karosses are obviously supple and the skins must have received some form of preparation prior to being trimmed and sewn together. This is in apparent contradiction to Owen's (1833) comment, but nevertheless essential to prevent rapid disintegration of the skin and loss of feathers through rotting (R. Rau, South African Museum, pers. comm.). It is more likely, therefore, that the skins were prepared. Flies would be attracted to the wearers' bodies, which would have been well-greased (Rudner 1982: 116 ff.), as well as to raw skins.

From the drawing it is estimated that some fifty pelts would be required to make up a full kaross. It is of interest to note that Nama Hottentot informants report that forty similar-sized hyrax (*Procavia capensis*) pelts are used to make a blanket (often described as a kaross) approximately 1,20 m × 1,60 m in area. One informant also described how hyrax skins were softened by hand and their raw

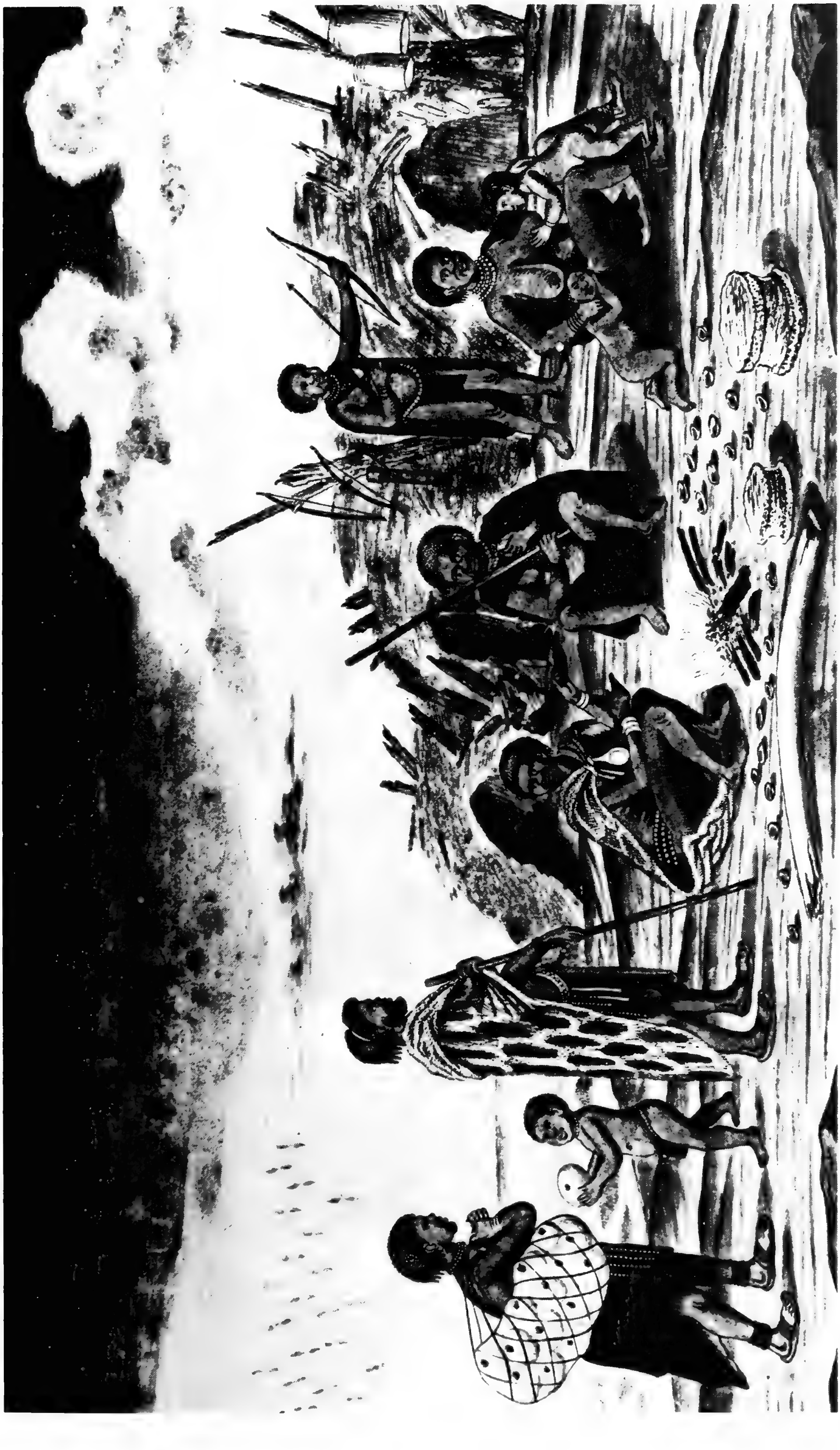

Fig. 6. Nama people on the coast near the mouth of the Orange River in 1779 (Gordon Collection No. 93, photograph courtesy of the Cape Archives). Note the colour and shape of the pelts and the texture of inner and outer surfaces of the karosses worn by the figures third and fourth from the left. They differ markedly from the skin garments worn by the other people.

sides were cleaned by means of little stones (L. Webley, University of Stellenbosch, pers. comm.).

Other illustrations by Gordon (Gordon Collection Nos. 84, 91, Cape Archives) appear to depict similar karosses, the first of these illustrations including what appear to be aprons made of a single penguin skin. These are not as convincing as those illustrated in Figure 6, and were from inland observations. However, the latter point, while relevant, need not present a problem, as it is well known that Khoisan people moved over great distances.

DISCUSSION

The fact that relatively few penguin bones occur can be explained by the size of the excavated sample. It is relevant that although relatively few bones ever show evidence of cutting, all penguin humerus fragments recovered and most of the tibiotarsus fragments show cut-marks. Furthermore, according to Thackeray's (1979) report on the earlier sample, penguins are the most common bird in the sample, in a proportion of 3 to 1.

The occurrence of penguin remains in midden accumulations has hitherto been assumed to indicate that these birds were eaten by the occupants of a site (Avery 1977; Thackeray 1979). However, penguin skins would make excellent pelts provided that they were preserved and softened; the skin is relatively thick and durable and the short feathers would provide good insulation. In order to preserve and soften them, the minimum of preparation required would involve scraping away the subcutaneous fat and other tissue adhering to the skins and working them to make them supple enough to be worn. Suitable scraping artefacts such as the small convex scrapers that occur in large numbers on the site would be essential to achieve this. In addition, experience from skinning a number of avian species and Cape fur seals taken from beaches indicates that even modern cutting instruments are rapidly blunted both by the presence of sand and by the resistance offered by feathers and thick fur. It may be predicted, therefore, that prehistoric skinning and scraping would have required regular sharpening and discarding of stone artefacts. Examination of the artefacts for wear traces would be a worthwhile test of this postulation.

Although there are instances of small numbers of penguins breeding on the mainland in localities where they are protected from predators (Finkeldey 1984), penguins are not normally accessible on the coast, as from choice they breed, and usually come ashore, on offshore islands. The Lüderitz Peninsula (Fig. 1), however, is close to a number of islands on which penguins breed or may have bred in the past (Rand 1963; Shaughnessy 1984). There are also other penguin colonies to the north and south of the area shown. Penguins do sometimes rest on the shore, moreover, and proximity to large breeding colonies would result in larger numbers doing this and thus being accessible. Mienertzhagen (1950) comments that large numbers of non-breeding individuals occurred on the shore and in the water opposite Halifax Island. The lack of an adult stripe on the

karosses depicted by Gordon suggests that the people were catching inexperienced immature birds, which often occur alive on beaches (pers. obs.) and are, therefore, more easily taken. Schultze (1907: 185) mentions Nama people catching immature penguins on beaches.

CONCLUSION

Although evidence is limited it is considered that skinning presents the best alternative to explain the location and nature of the cut-marks on the specimens. It is further postulated that the occurrence of relatively high frequencies of small convex scrapers and backed bladelets, and some segments, is correlated with the skinning and preparation of penguin pelts.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

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GRAHAM AVERY

LATE HOLOCENE USE OF PENGUIN SKINS: EVIDENCE FROM A COASTAL SHELL MIDDEN AT STEENBRAS BAY, LÜDERITZ PENINSULA, SOUTH WEST AFRICA–NAMIBIA

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CAPE TOWN

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ASPECTS OF THE MORPHOLOGY OF THE ENDEMIC SOUTH AFRICAN CYPRAEIDAE WITH A DISCUSSION OF THE EVOLUTION OF THE CYPRAEACEA AND LAMELLARIACEA

By

TERRENCE M. GOSLINER
&
WILLIAM R. LILTVED

Cape Town Kaapstad

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Fig. 1. Living animals. A. *Cypraea fuscorubra* Shaw, 1909. B–C. *Cypraea algoensis* Gray, 1825. D–E. *Cypraea coronata* (Schilder, 1930). F. *Cypraea fuscodentata* Gray, 1825. G. *Cypraea edentula* Gray, 1825, with egg mass. H. Advanced embryo of *Cypraea algoensis* Gray, 1825.

ASPECTS OF THE MORPHOLOGY OF THE ENDEMIC SOUTH AFRICAN CYPRAEIDAE WITH A DISCUSSION OF THE EVOLUTION OF THE CYPRAEACEA AND LAMELLARIACEA

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(With 35 figures and 1 table)

[*MS accepted 24 September 1984*]

ABSTRACT

Aspects of the morphology of eight endemic species of South African Cypraeidae are studied and the variability of various characters within the family is discussed. Lack of knowledge at present prevents the subdivision of *Cypraea* into monophyletic genera or subgenera. A discussion of the phylogeny of the Cypraeacea and Lamellariacea confirms that the Triviidae are allied to the Lamellariidae rather than the Cypraeidae and Ovulidae. Examination of *Pedicularia californica* reveals that it is most closely allied to the Ovulidae. The three species of South African Cypraeidae that have been studied exhibit direct development and lack a free-swimming veliger larva.

CONTENTS

INTRODUCTION

The family Cypraeidae is one of the most widely studied groups of molluscs, yet surprisingly little is known about its morphology and biology. The vast amount of systematic work within the Cypraeidae has been based largely on conchological features with little attempt to correlate these with characters of the

* The authors have contributed equally to the content of this publication.

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living animal, radula, or internal morphology of the nervous and reproductive systems. The shores of southern Africa are rich in *Cypraea* species, and are particularly noteworthy owing to the large number of endemic species. Burgess (1970) listed ten endemic species from southern Africa. Since then *Cypraea cruickshanki* Kilburn, 1972, *C. iutsui* (Shikama, 1974), *C. lisetae* Kilburn, 1975, and *C. connelli* Liltved, 1983, have been described, although the validity of some of these species has been questioned. *Cypraea broderipi* has more recently been found from Somalia (Derry 1981), Mauritius and Réunion Island (Whatmore 1981) and can no longer be considered endemic. Morphological studies of the endemic species of South African *Cypraea* are limited to the illustration of the radulae of *C. fultoni* and *C. capensis* (Kilburn & Aiken 1972), *C. iutsui* (Barnard 1963, as globose form of *C. fuscorubra*) and *C. cruickshanki* (Kilburn, 1972), and a brief description of the female reproductive system of *C. capensis* (Kilburn & Aiken 1972).

Recent collections, by means of SCUBA diving along the South African coast from the Cape Peninsula to Algoa Bay, have yielded living specimens of five additional species of *Cypraea*. Their morphology is described here together with that of preserved specimens of *C. capensis, C. cruickshanki* and *C. iutsui*. The taxonomic status of the South African endemic Cypraeidae is reviewed.

Many authors (e.g. Schilder 1936) have suggested that *Cypraea* be subdivided into numerous genera or subgenera while others have maintained that the species should remain united within a single genus. The relative strengths and weaknesses of these arguments are presented.

There has also been considerable question as to the relationships of the various families comprising the Cypraeacea and Lamellariacea, particularly regarding the status of the Triviidae and *Pedicularia*. The morphology of these taxa is reviewed and the phylogeny of these superfamilies is discussed.

MORPHOLOGICAL DESCRIPTIONS

Cypraea fuscorubra Shaw, 1909

Figs 1A, 2–8, 33A

Cypraea similis Gray, 1831: 36, *non* Gmelin, 1791.
Cypraea fuscorubra Shaw, 1909: 302.
Cypraea gondwanalandensis Burgess, 1970: 31, pl. 1 (figs A–A2).

Material

Specimens (SAM–A35990) were collected at several localities on the Atlantic coast of the Cape Peninsula from 25 to 48 m depth. A single specimen (SAM–A35991) was collected from Danger Point in 30 m of water.

Distribution

Cypraea fuscorubra is known from the Atlantic coast of the Cape Peninsula to Cape Agulhas.

Shell

The shell (Fig. 2) is ovoid, 28–40 mm in length. The spire is generally not umbilicate and the protoconch is generally covered by a callus. The labrum has a dull finish with 17–18 coarse brown teeth. The aperture is moderately narrow, widest anteriorly. The columella has 18–24 teeth, which are finer than the labral teeth and do not extend beyond the aperture. The fossula is straight to convex with three or four denticles. The dorsum is thickly calcified. The dorsal surface is cream, slate-grey or mauve and is densely spotted with a reticulate pattern of spots. The base is thick, cream in colour with brown spotting.

Living animal (Fig. 1A)

The foot is thick and wide, shortened and rounded posteriorly. The foot and siphon are white in colour and their dorsal surface may be ornamented with sparse black spots or stippling. The smooth siphon is short and wide, recurved and slightly uneven at the apex. The yellow tentacles are straight and slightly tapered. The opaque mantle is smooth but occasionally it has a slightly granular texture. Typically the ground-colour of the mantle is red or whitish but occasionally it may be cream with black longitudinal lines forming a 'finger-print' pattern of parallel lines.

Mantle complex (Fig. 3)

The mantle cavity is directed towards the right side of the body. The ctenidium is large, consisting of approximately 200 triangular plicae. The triradiate osphradium is situated anterior to the ctenidium and consists of numerous leaflets. Posterior to the ctenidium, on the left side of the body, is the vascular kidney. At the junction of the ctenidium and kidney is the two-chambered heart. Near the opening of the mantle cavity, at the level of the kidney, is the hypobranchial gland, which consists of 11 plicae.

Digestive system

The large, muscular buccal mass comprises the bulk of the anterior portion of the body (Fig. 4). From it extend the wide, glandular oesophagus and the coiled radular sac. The salivary glands are fused and possess a pair of ducts that pass through the nerve ring and the buccal mass adjacent to its junction with the oesophagus. The oesophagus narrows into the intestine, which forms a short loop, the stomach. There are two ducts emanating from the stomach to the large, granular digestive gland. No caecum was observed. The intestine curves to the right beyond the stomach and terminates at the anus, near the opening of the mantle cavity (Fig. 3).

The buccal mass contains a pair of flexible jaws (Fig. 5), which almost completely dissolve when placed in 10 per cent sodium hydroxide. The taenioglossate radula is a narrow, elongate ribbon, about two-thirds of which is contained within the radular sac at the posterior end of the buccal mass. The

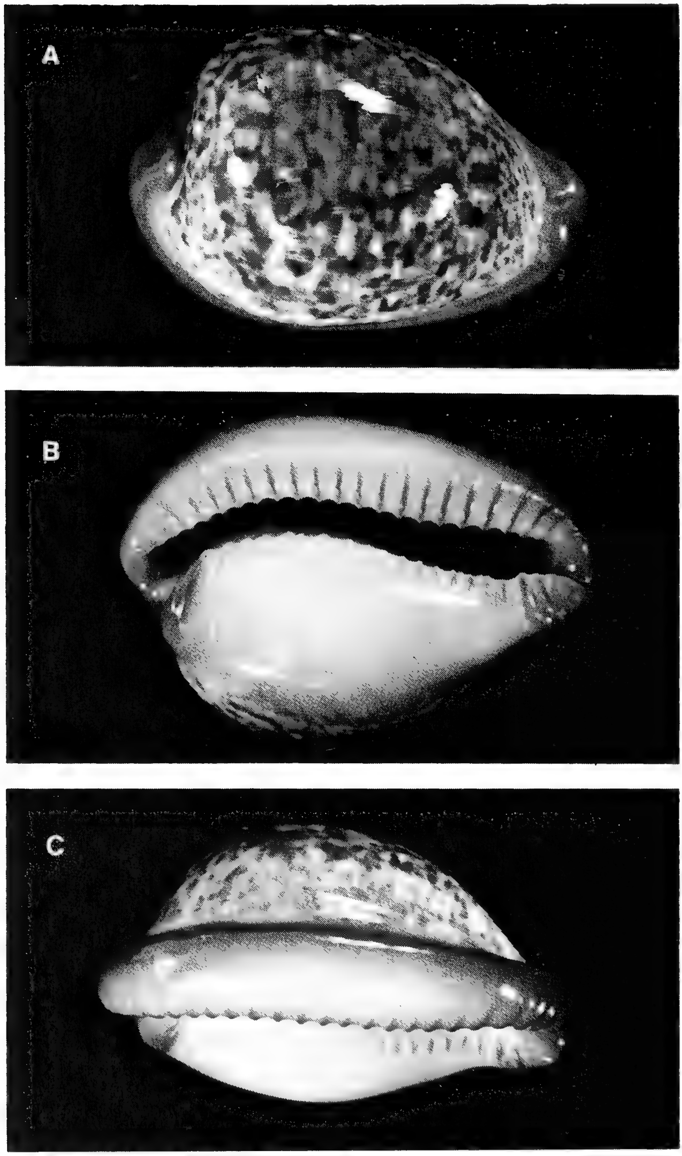

Fig. 2. *Cypraea fuscorubra* Shaw, 1909. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

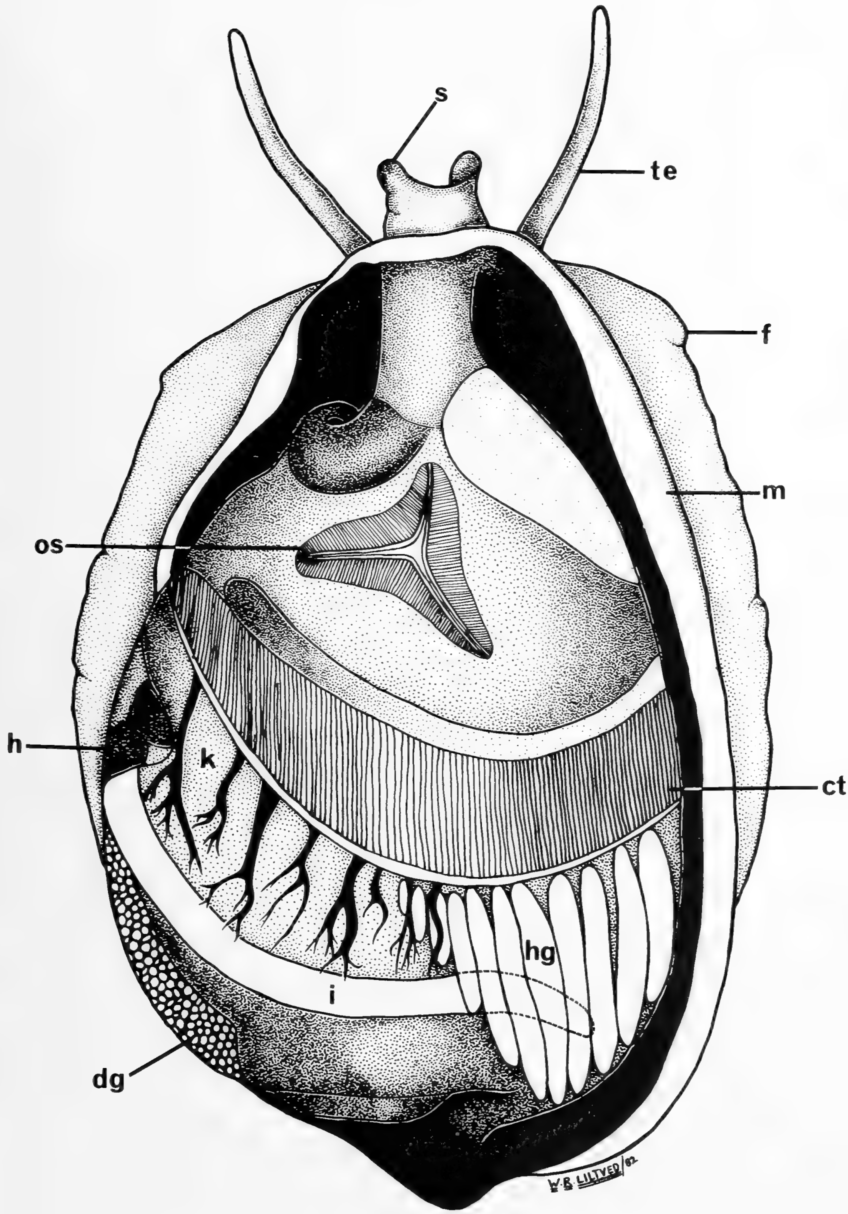

Fig. 3. *Cypraea fuscorubra* Shaw, 1909. Mantle complex.

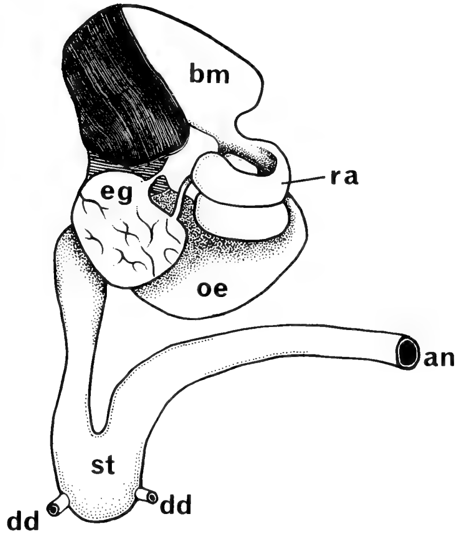

Fig. 4. *Cypraea fuscorubra* Shaw, 1909.
Digestive tract.

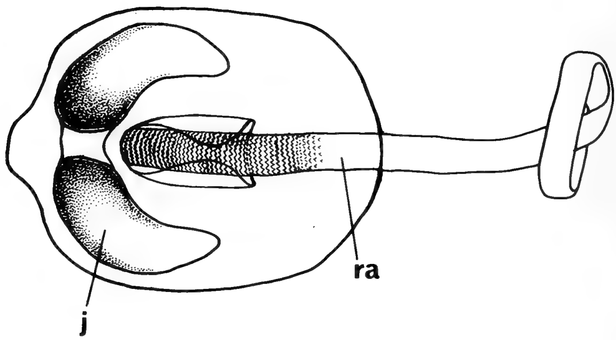

Fig. 5. *Cypraea fuscorubra* Shaw, 1909. Jaws.

radula (Figs 6, 33A) consists of 93–96 rows of teeth. Each row contains three lateral teeth on either side of the rachidian tooth. Each tooth has a small rounded denticle on either side of the strong central cusp. There is a thin outer margin and a strong, centrally emarginate base to the rachidian tooth.

Central nervous system (Fig. 7)

The central nervous system is modified from the typical prosobranch plan. It is highly cephalized and asymmetrical with most ganglia situated to the left of the oesophagus. The paired cerebral ganglia are closely appressed to each other,

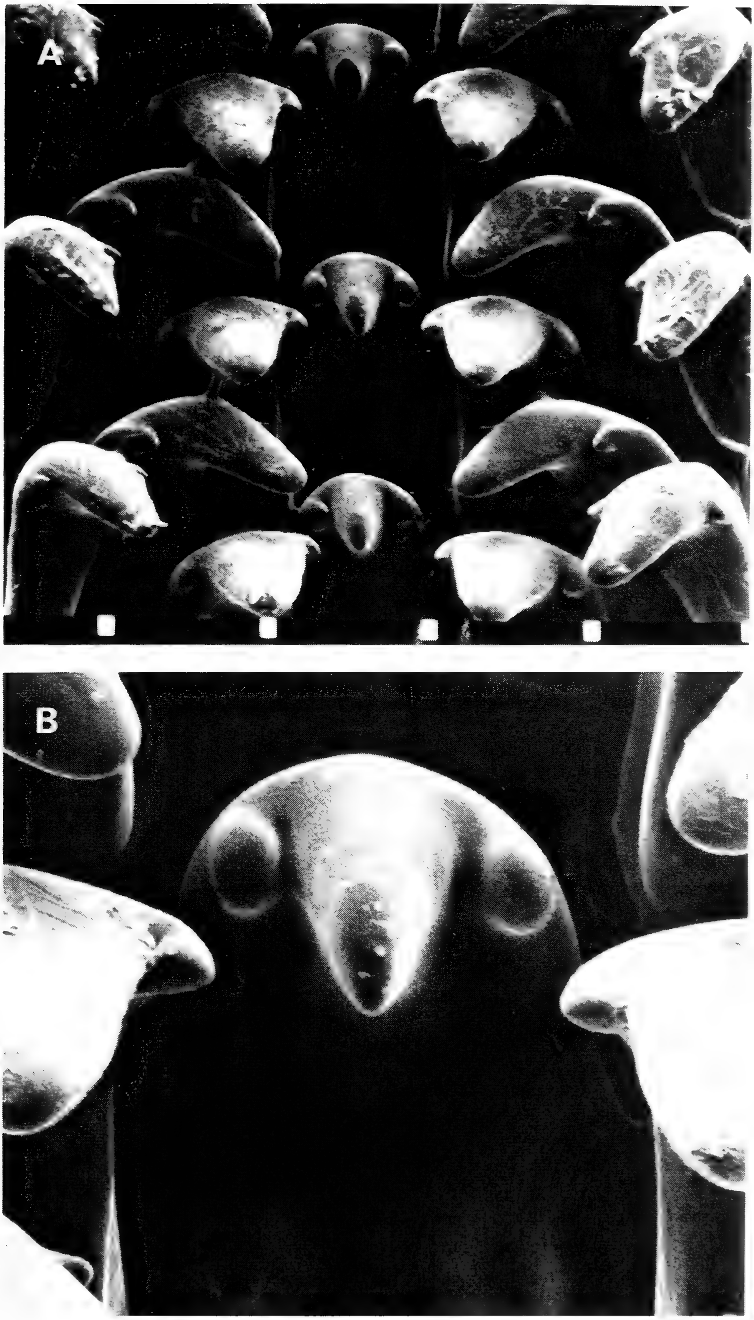

Fig. 6. *Cypraea fuscorubra* Shaw, 1909. Scanning electron micrographs of teeth. A. Entire width of radula. B. Central region.

without a distinct commissure between them. From the cerebral ganglia a pair of nerves emanates anteriorly and joins the paired buccal ganglia on either side of the junction of the oesophagus and buccal mass. Adjacent and slightly dorsal to the cerebral ganglia are the pleural ganglia. From their anterior side a pair of nerves connects with the supraintestinal ganglion, situated anterior to the cerebral ganglion at the base of the osphradium, on the left side of the mantle cavity. The nerve between the left pleural and supraintestinal ganglia represents a zygoneurous connective. Nerves from the supraintestinal ganglion innervate the osphradium and ctenidium, and extend to the posterior end of the body cavity. From the posterior side of the cerebral and pleural ganglia extend the pedal connectives, which are fused for most of their lengths. The pedal connectives join the elongate pedal ganglia, which are fused anteriorly without a distinct commissure. These ganglia are embedded in the muscular tissue of the foot. There are nerves emerging from the outer side of most of the length of the pedal ganglia and ladder-like connectives between the two ganglionic masses. A thick, elongate nerve emerges from the posterior end of the left pleural ganglion and

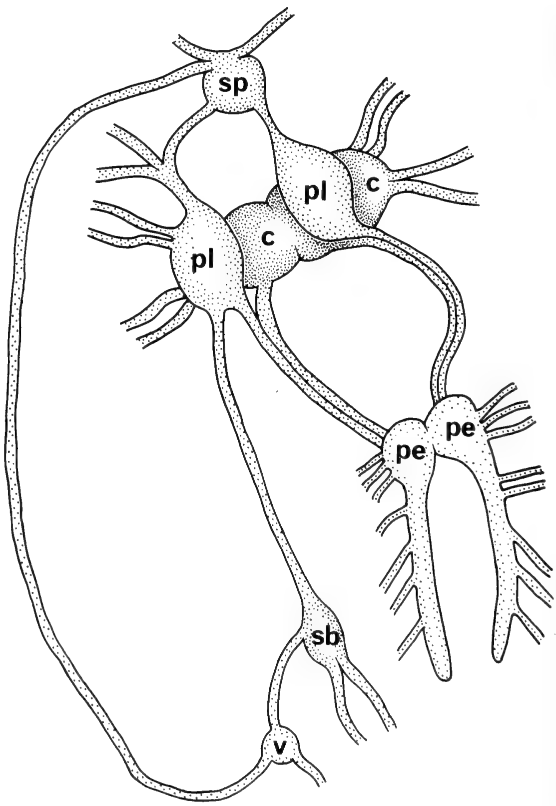

Fig. 7. *Cypraea fuscorubra* Shaw, 1909.
Central nervous system.

joins the subintestinal ganglion near the posterior end of the body cavity. Three large nerves emerge from the posterior portion of the subintestinal ganglion. The nerve at the left side of the ganglion continues posteriorly and connects with the small visceral ganglion, at the base of the genital mass, near the posterior limit of the oesophagus. The visceral ganglion branches posteriorly to innervate the genital mass and anteriorly gives rise to the right lateral nerve cord, which continues anteriorly until it joins the supraintestinal ganglion.

Reproductive system

The animals are gonochoric. The female system (Fig. 8A) consists of a large, yellowish ovary, which interdigitates with the digestive gland. From the anterior

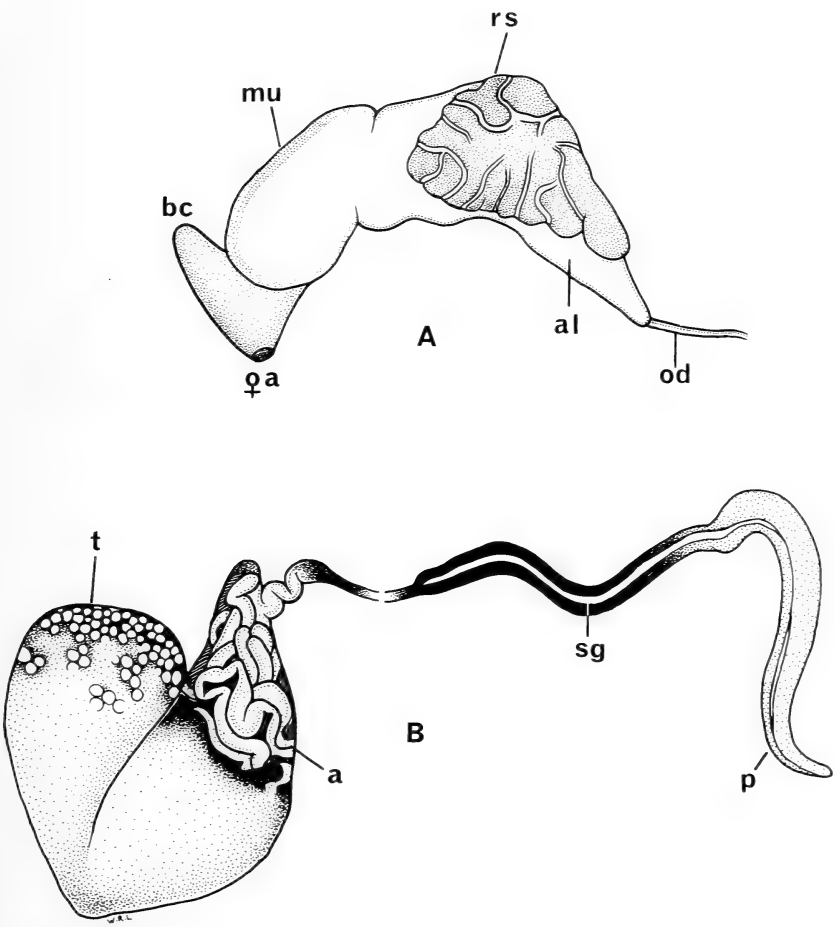

Fig. 8. *Cypraea fuscorubra* Shaw, 1909. A. Female reproductive system. B. Male reproductive system.

end of the ovary the narrow oviduct emerges. It widens into the albumen gland. On the anterodorsal surface of the albumen gland is the dark grey, glandular receptaculum seminis. Ventral to the receptaculum seminis is the narrow band of the membrane gland. Anteriorly, the bulk of the female gland mass is composed of the mucous gland (=capsule gland of Kay (1960*b*)). The mucous gland narrows anteriorly and joins the bulbous bursa copulatrix near the gonopore.

The male system (Fig. 8B) consists of a large testis with numerous acini. These empty into the elongate, highly convoluted ampulla (= seminal vesicle of Kay (1960*b*)). The ampulla narrows to a glandular, prostatic vas deferens with an opening near the entrance of the mantle cavity. From this opening a ciliated sperm groove connects the vas deferens to the tip of the muscular penis on the right side of the head.

Cypraea algoensis Gray, 1825

Figs 1B, C, H, 9–11, 32, 33B

Cypraea algoensis Gray, 1825: 498.

Material

Numerous specimens have been collected and studied from 20 to 48 m depth along the Atlantic coast of the Cape Peninsula (SAM–A35992), in 17–35 m depth in False Bay (SAM–A35993), and recorded from 30 m depth at Danger Point.

Distribution

Specimens have been collected along the south-western Cape coasts from Saldanha Bay on the Atlantic coast to Cape Agulhas. This species may extend as far north-east as Jeffreys Bay.

Shell

Conchologically *Cypraea algoensis* is variable but with some consistent and distinctive features. The adult shell (Fig. 9) ranges from 12 to 31 mm in length. The spire is generally not umbilicate and the protoconch may or may not be visible. The labrum is strongly developed with 14–21 fine white teeth, which extend across about half the width of the labrum. The narrow aperture is widened anteriorly and strongly curved posteriorly. There are 9–21 finely denticulate columellar teeth. The fossula is poorly developed or absent, occasionally with two or three denticles. The shell varies in shape from pyriform to globular. Globose specimens are generally characteristic of water deeper than 50 m, and are more heavily calcified.

Shells from the Atlantic coast of the Cape Peninsula are generally about one-third larger and have a flesh or orange ground-colour with fine brown dorsal spotting, while shells from False Bay to Cape Agulhas are normally smaller and may be dark purple with dark brown dorsal spots. The base of the shell and the teeth are always whitish and dark brown marginal spots are present.

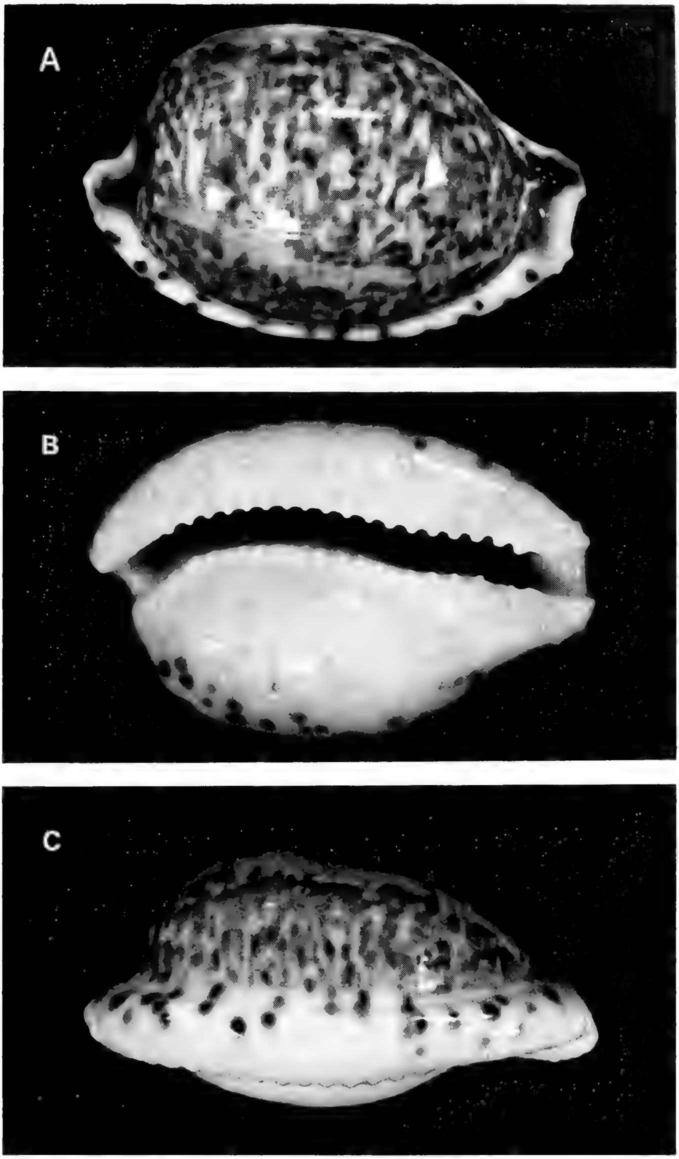

Fig. 9. *Cypraea algoensis* Gray, 1825. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

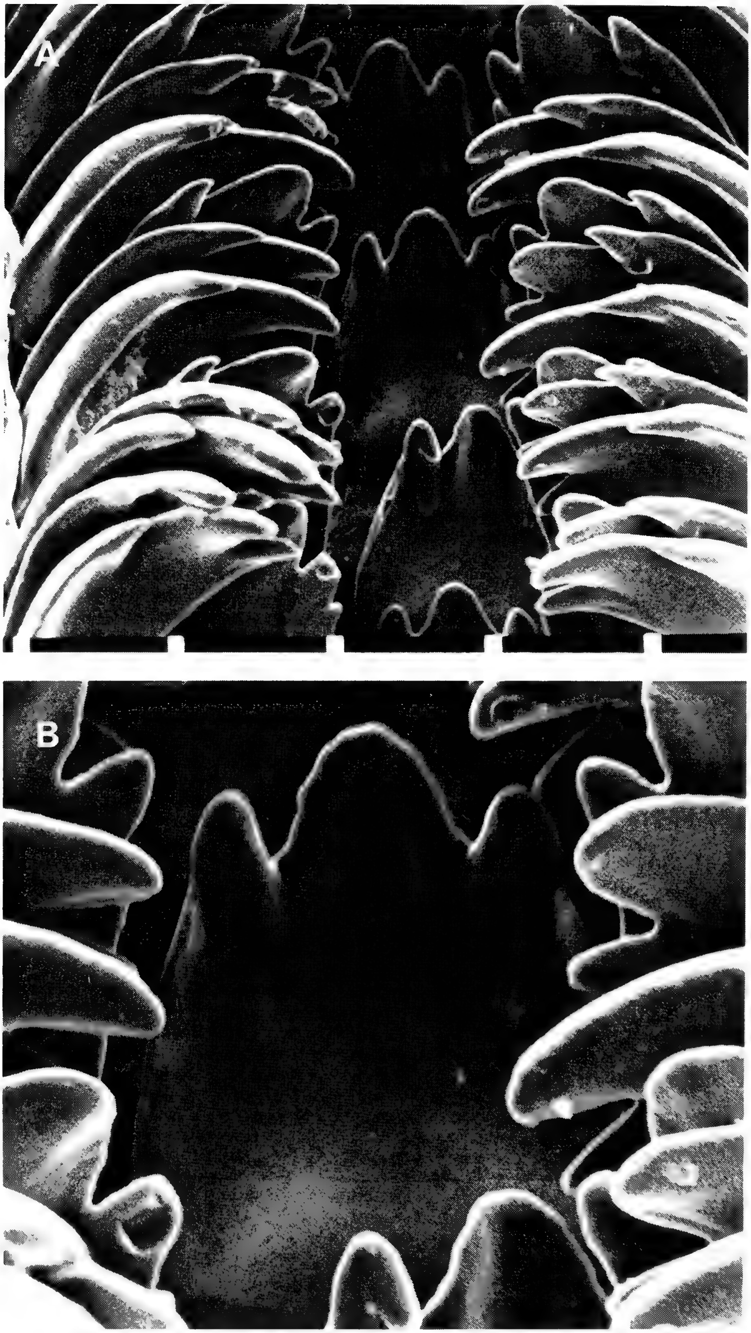

Fig. 10. *Cypraea algoensis* Gray, 1825. Scanning electron micrographs of radula. A. Entire width. B. Central region.

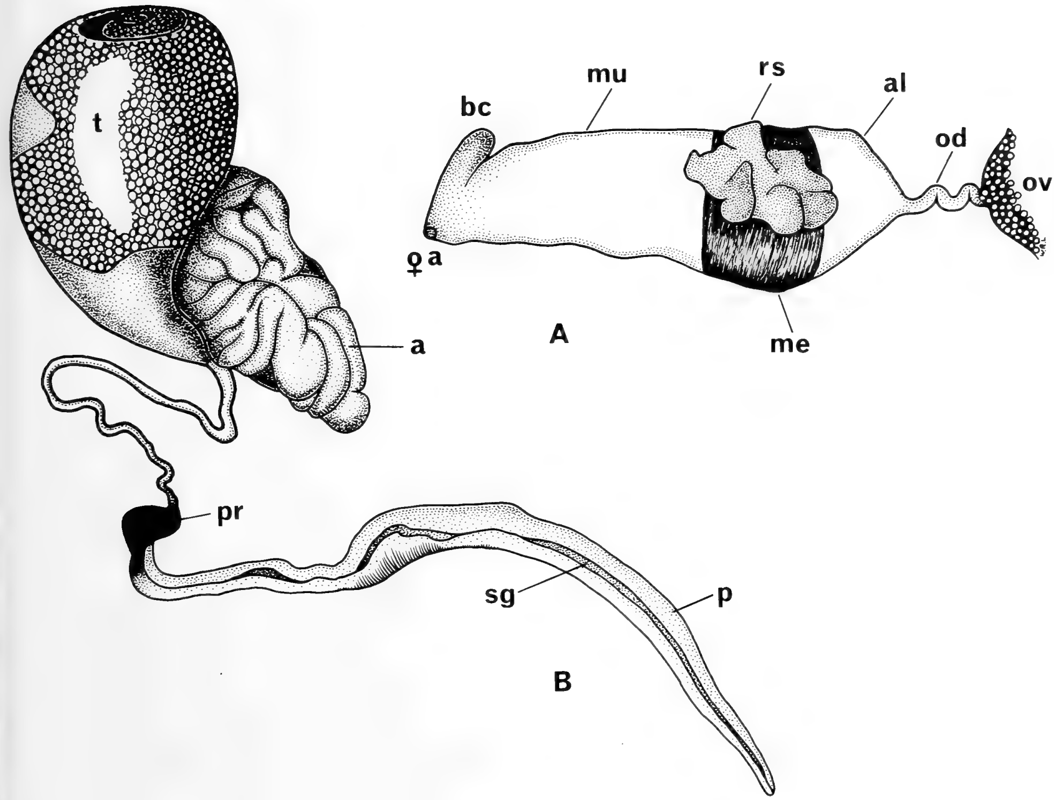

Fig. 11. *Cypraea algoensis* Gray, 1825. A. Female reproductive system. B. Male reproductive system.

Living animal (Fig. 1B, C)

The foot is short and thick, rounded posteriorly. Most commonly the foot is salmon-pink in colour but it may occasionally be white, and black spots may be present. Specimens from False Bay generally possess a dense pattern of black lines. The smooth siphon is white or black with a white apex; the tip is slightly thickened but smooth. The lemon-yellow tentacles are slender and slightly tapered. The mantle is salmon or translucent white, with finely stippled black specks, or marked with fine brown lines forming a 'finger-print' pattern. Specimens from False Bay to Cape Agulhas generally have a black mantle, which often possesses white wart-like or fleshy finger-like papillae.

Mantle complex

The arrangement of organs within the mantle complex is identical to that described for *C. fuscorubra*. The ctenidium consists of about 150 leaflets while the hypobranchial gland is composed of seven plicae.

Digestive system

The digestive organs are arranged as in *C. fuscorubra*. The radular formula is 77–91 × 3.1.3. The rachidian tooth (Figs 10, 33B) is broad and rectangular with a small central cusp flanked by a pair of oblong cusps. The base of the rachidian tooth is short with a slight medial indentation. The lateral teeth are also broad with three cusps. The central cusp is shortest on the inner lateral tooth and longest on the outermost.

Central nervous system

The arrangement of ganglia is identical to that described for *C. fuscorubra*.

Reproductive system

The configuration of both the male and female reproductive organs is similar to that described for *C. fuscorubra*. The only significant differences are the proportionately smaller receptaculum seminis in the female (Fig. 11A) and the discrete prostate in the male of *C. algoensis* (Fig. 11B).

Cypraea coronata (Schilder, 1930)

Figs 1D–E, 12–15, 33C

Luponia coronata Schilder, 1930: 113, text-fig.
Cypraeovula gloriosa Shikama, 1971: 101.

Material

Five specimens (SAM–A35988) were examined from the Atlantic coast of the Cape Peninsula where they were collected in 25–48 m of water. A single specimen was also recorded from 30 m depth off Danger Point.

Distribution

Cypraea coronata is known from the Atlantic coast of the Cape Peninsula to Transkei.

Shell (Fig. 12)

The shell varies in length from 26 to 36 mm and is pyriform with closely spaced growth lines. The spire is slightly umbilicate with a well-developed callus covering the protoconch. The prominent labrum and thickened columellar margin are tuberculate. Tubercles may be absent in juvenile specimens and occasionally in adults. The aperture is narrow, widening slightly anteriorly and curving posteriorly. There are 18–20 coarse teeth on the labrum, some of which are occasionally fused. The anteriormost and posteriormost teeth may extend over the labrum and fuse with the tubercles. There are 16–22 columellar teeth. The mid-columellar teeth are fine and become coarser and pigmented towards either end of the columella. These anterior and posterior columellar teeth extend on to the columella. The dorsal surface of the shell is mauve, slate-grey or cream with transverse rows of olive-green or brown pigment. This pigment is usually

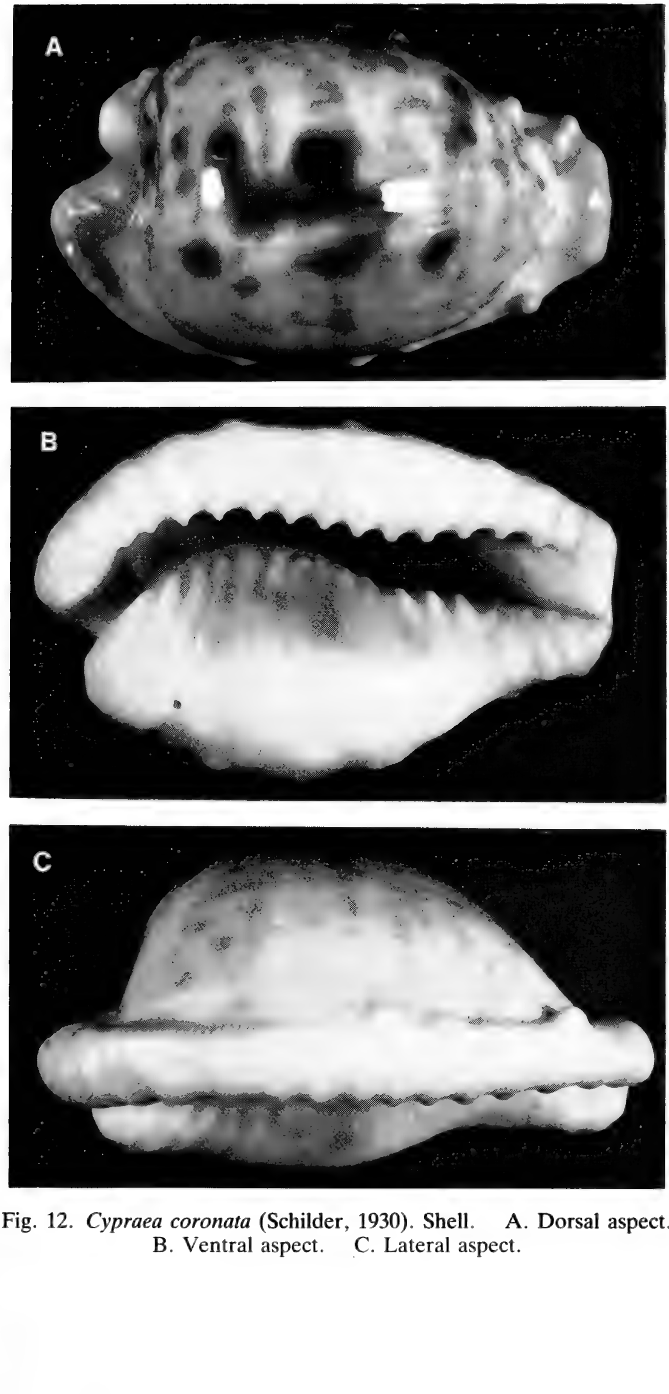

Fig. 12. *Cypraea coronata* (Schilder, 1930). Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

overlaid with blotches of olive-green or chestnut-brown, which may cover most of the dorsal surface of the shell.

Living animal (Fig. 1D–E)

The external morphology of *Cypraea coronata* is less variable intraspecifically than in any other species of endemic Cypraeidae in southern Africa. The creamy-white foot is thick, short and fleshy. It is thickened anteriorly. The siphon is usually sparsely papillate throughout with minute wart-like papillae, and is thickened at its tip. The lemon-yellow tentacles are slender and gradually taper; the tips are blunt and slightly darker in colour. The mantle is covered with white wart-like papillae approximately 1 mm in diameter. Between these papillae are more numerous smaller papillae about 0,2 mm in diameter. The margins of the mantle lobes are covered with a reticulate pattern of dark-brown or black pigment. This pigment does not extend on to the surface of the papillae. The intensity of the pigment decreases away from the margins of the lobes and is replaced by pink pigment. Specimens with a black or translucent white mantle and white papillae have been encountered but are rare.

Mantle complex

The arrangement of organs within the mantle complex is identical to that described for *C. fuscorubra*. The ctenidium consists of approximately 200 leaflets while the hypobranchial gland contains four plicae.

Digestive system

The only significant feature of the digestive system distinguishing *C. coronata* from *C. fuscorubra* is the morphology of the radula. The radular formula is $95 \times 3.1.3$ in one specimen examined. The rachidian teeth (Figs 13, 33C) are square in shape rather than trapezoidal. The central cusp is triangular and is flanked by a pair of rounded lateral denticles. At the base of each of the lateral denticles is a small secondary denticle. The base of the rachidian tooth is small and medially slightly emarginate. The lateral teeth (Fig. 14) also possess a pair of primary denticles on either side of the elongate central cusp and a secondary cusp at the base of the inner primary denticle of the first two laterals. The bases of the lateral teeth are proportionately smaller than in *C. fuscorubra*.

Central nervous system

The configuration of the ganglia is identical to that described for *C. fuscorubra*.

Reproductive system

The male system is identical to that described for *C. fuscorubra*. The female system (Fig. 15) is only slightly different; the receptaculum seminis of *C. coronata* appears to be more ramified than that of *C. fuscorubra*.

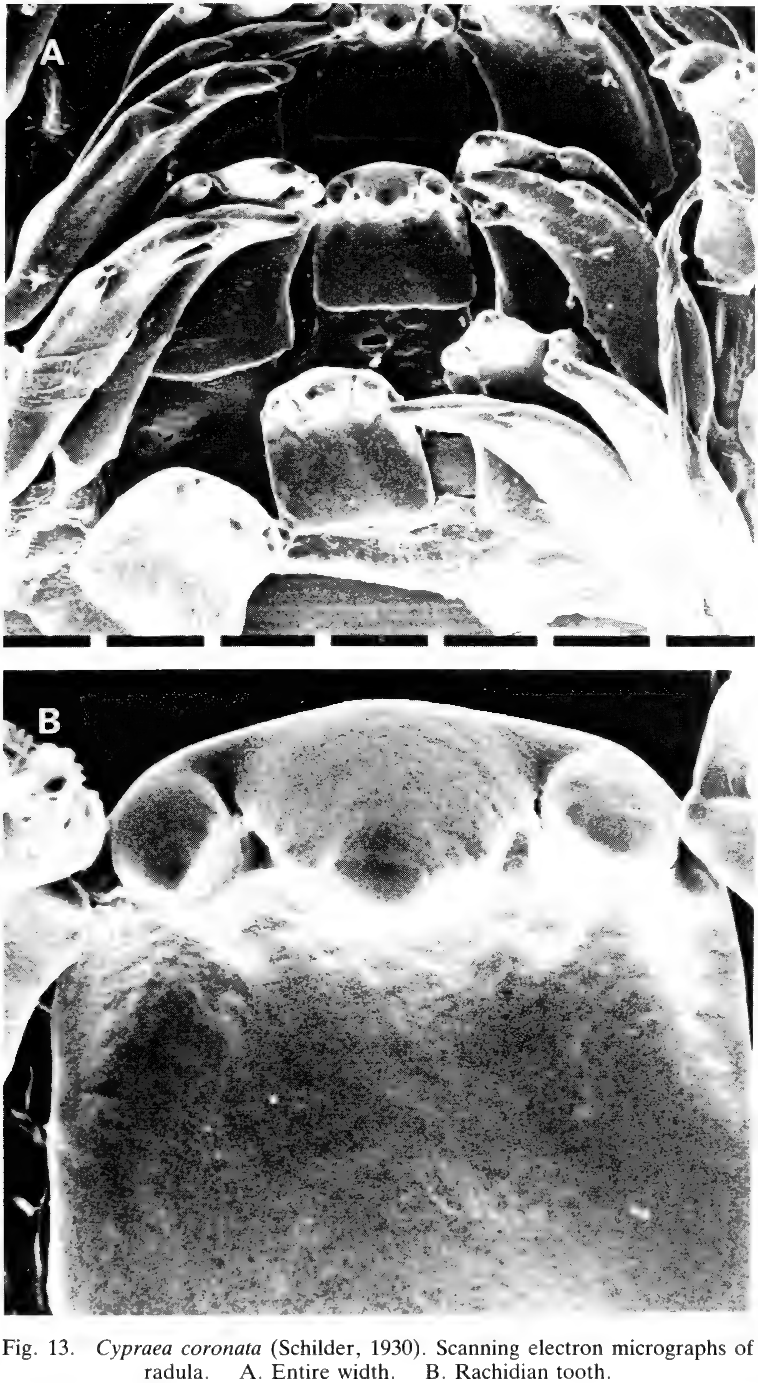

Fig. 13. *Cypraea coronata* (Schilder, 1930). Scanning electron micrographs of radula. A. Entire width. B. Rachidian tooth.

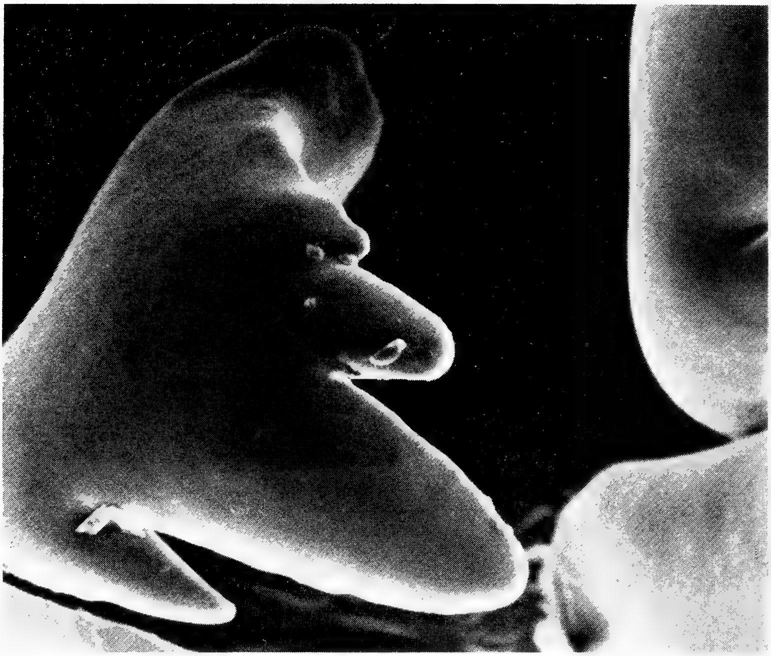

Fig. 14. *Cypraea coronata* (Schilder, 1930). Scanning electron micrograph of inner lateral tooth.

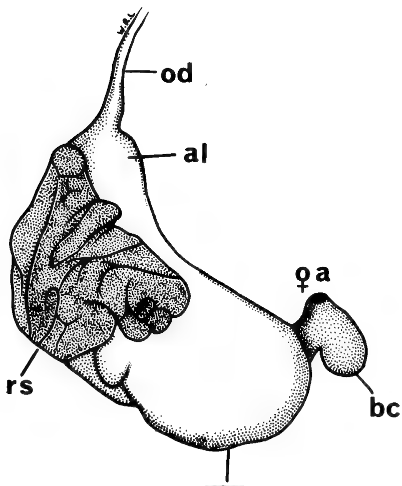

Fig. 15. *Cypraea coronata* (Schilder, 1930). Female reproductive system.

Cypraea fuscodentata Gray, 1825

Figs 1F, 16–18, 33D

Cypraea fuscodentata Gray, 1825: 499.

Material

Ten specimens (SAM–A35989) were collected from 6 to 35 m in False Bay, Cape Peninsula.

Distribution

Cypraea fuscodentata has been collected from False Bay to Jeffreys Bay.

Shell

The shell (Fig. 16) is cylindrical to pyriform, ranging in length from 21 to 44 mm. The spire is umbilicate and the protoconch is generally obscured. The labrum has 15–19 coarse, dark-brown teeth. The aperture is very narrow. The 15–20 coarse columellar teeth extend from the aperture across most of the width of the columella. The fossula is straight or convex, without denticulations. The dorsal surface is thickly calcified with a cream or grey ground-colour and a dense pattern of brown spots. The margins of the shell may be cream, brown or purple.

Living animal (Fig. 1F)

The broad foot is short and posteriorly rounded. The siphon is recurved at the smooth tip and may be white or black with a white tip. The tentacles are elongate and slightly tapered, and yellow to orange in colour. The coloration of the mantle and foot is exceedingly variable. It may be black, white, orange, brown or red in individuals from the same population. Sparse papillae of variable shape may be present or absent from the outer surface of the mantle. When present the papillae tend to be denser near the margins of the mantle.

Mantle complex

The organs of the mantle cavity are arranged identically to those described for *C. fuscorubra*. In a juvenile specimen the ctenidium consists of about 150 leaflets and the hypobranchial gland of seven plicae.

Digestive system (Figs 17, 33D)

The organs of the digestive system are arranged identically to those described for *C. fuscorubra*. The rachidian tooth of *C. fuscodentata* has a pair of distinct ridges on the inner face, which are absent in *C. fuscorubra* and *C. coronata*. The radular formula in one specimen is 83 × 3.1.3. The central cusp is short, as are the oblong adjacent cusps. The central cusp of each of the lateral teeth is elongate, as are the smaller adjacent cusps.

Central nervous system

The arrangement of ganglia is identical to that of *C. fuscorubra*.

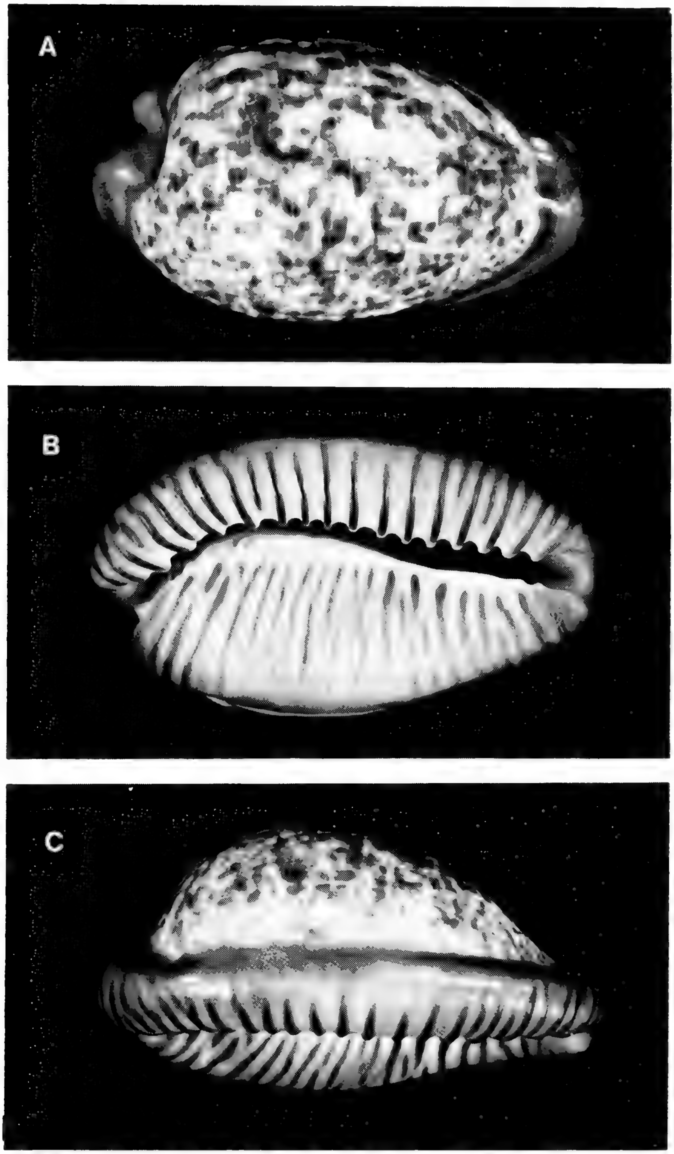

Fig. 16. *Cypraea fuscodentata* Gray, 1825. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

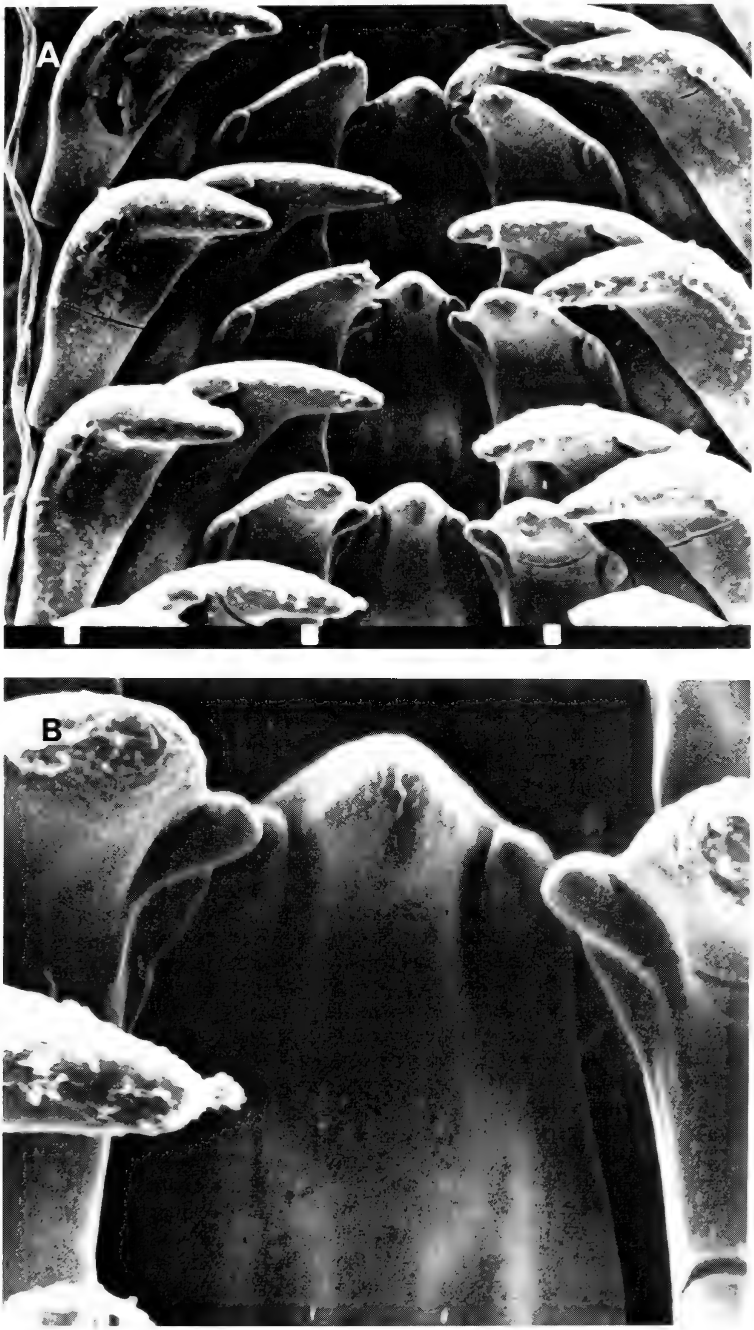

Fig. 17. *Cypraea fuscodentata* Gray, 1825. Scanning electron micrographs of radula. A. Entire width. B. Central region.

Reproductive system

Both the female and male systems are arranged in the manner described for *C. fuscorubra* with the exception that the receptaculum seminis is far more elaborate in *C. fuscodentata* (Fig. 18).

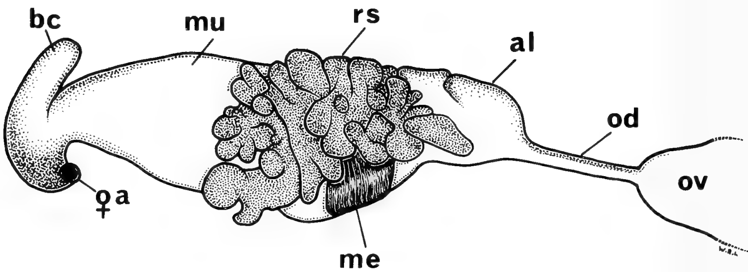

Fig. 18. *Cypraea fuscodentata* Gray, 1825. Female reproductive system.

Cypraea capensis Gray, 1828

Figs 19–20, 33E

Cypraea capensis Gray, 1828: 573.

Material

The single specimen (SAM–A35995) examined was removed from the stomach of a fish collected in Algoa Bay.

Distribution

Cypraea capensis is known from the eastern Cape Province and Transkei from Jeffreys Bay to Port St. Johns, and from deep water off Natal.

Shell (Fig. 19)

The shell is elongate, pyriform, from 22 to 39 mm in length. The spire is umbilicate and the protoconch may be obscured by a callus. The labrum is ornamented with 20–28 fine, brown teeth, which extend on to and across the dorsum and columella as transverse ribs. These ribs continue on to the columella, where they merge with the columellar and fossular denticles. The fossula is convex. The dorsum may be brown, grey or purple in colour, and may or may not be ornamented with dark brown mottling.

Living animal

The only description of the external morphology of *C. capensis* is that of Kilburn & Aiken (1972). In the specimen they described the foot and tentacles were bright orange-yellow and the mantle was brownish with dark spots and faint white lines.

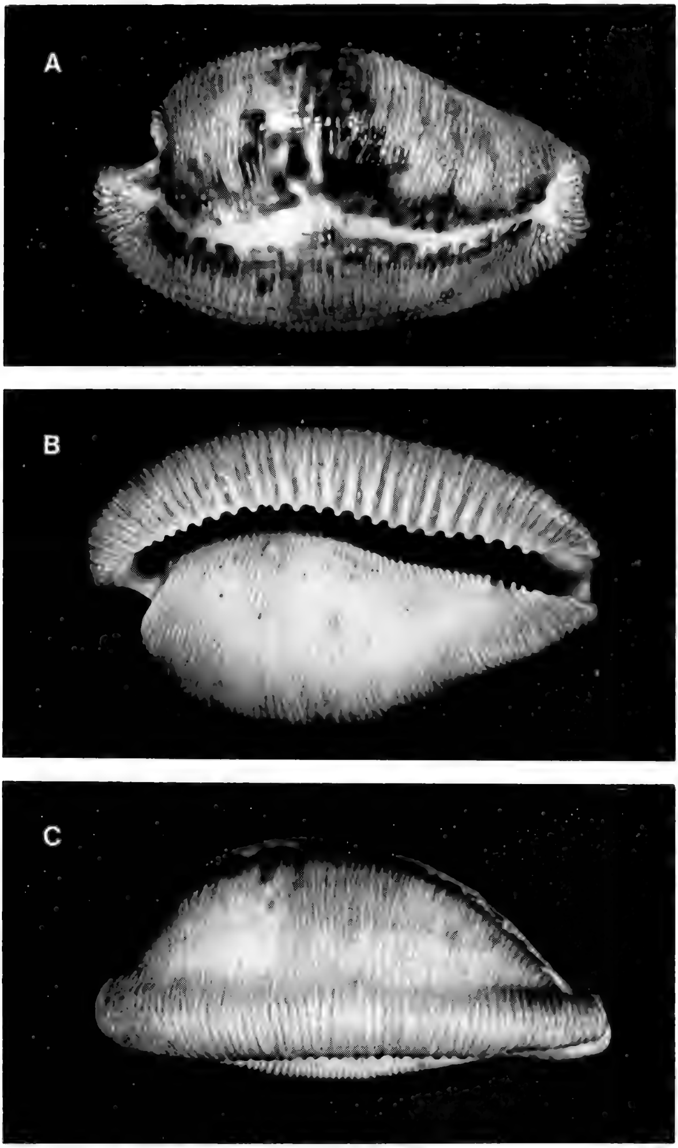

Fig. 19. *Cypraea capensis* Gray, 1828. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

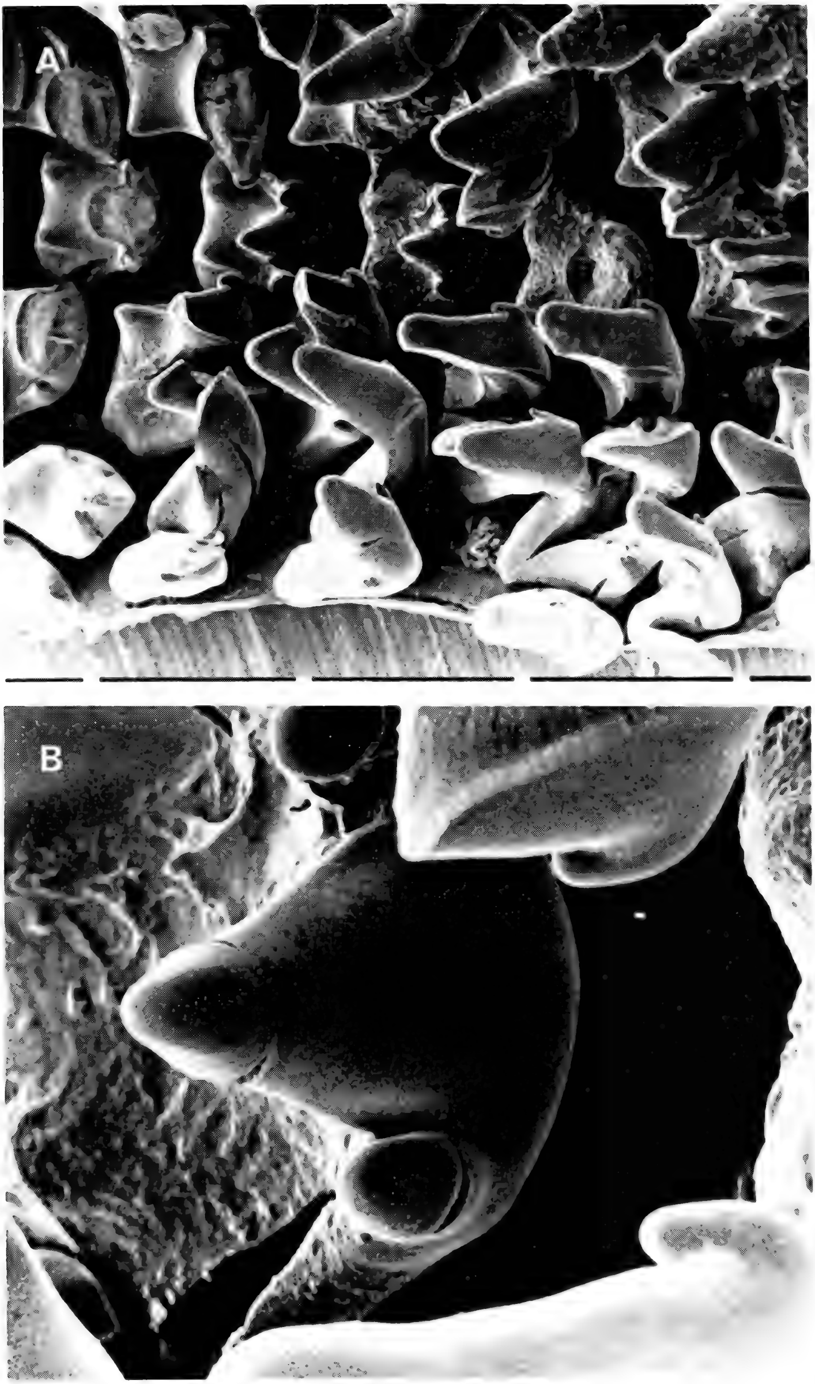

Fig. 20. *Cypraea capensis*. Scanning electron micrographs of radula.
A. Entire width. B. Central region.

Mantle complex

Owing to the desiccation of the specimen details of the mantle complex could not be determined.

Digestive system (Figs 20, 33E)

The radular formula is $76 \times 3.1.3$. The rachidian tooth is trapezoidal with a well-developed triangular central cusp. There is a pair of strong ridges on the inner side of the rachidian tooth. The base of the rachidian tooth is large and deeply emarginate. The lateral tooth possesses an elongate cusp and rounded adjacent denticles.

Central nervous system

Although the specimen was poorly preserved it was possible to determine that there is an elongate lateral nerve cord present between the left pleural and subintestinal ganglia as in *C. fuscorubra*. The pedal ganglia are also elongate.

Reproductive system

The specimen was not sufficiently preserved to examine the reproductive system. Kilburn & Aiken (1972) stated that the female specimen they examined had a glandular receptaculum seminis and a bursa copulatrix. However, it is unclear whether the receptaculum consists of small glands as described by Kay (1960*a*) or if it is lobate as in the other South African species examined in this study.

Cypraea edentula Gray, 1825

Figs 1G, 21–23, 33F

Cypraea algoensis var. *edentula* Gray, 1825: 498.

Material

One specimen destroyed by dissection was collected off the Sunday's River Mouth north of Port Elizabeth in 48 m of water. A second specimen (SAM–A35994) was collected from 12 m in Algoa Bay.

Distribution

Cypraea edentula has been collected from Tsitsikama Coastal National Park to the south-western Transkei.

Shell (Fig. 21)

The shell of *Cypraea edentula* varies in length from 12 to 33 mm and is highly variable in shape and coloration. The spire may be slightly umbilicate or produced. The protoconch is usually visible. Generally, labral and columellar teeth are entirely absent. Some specimens have poorly-developed denticles on the labrum but these are normally limited to the anterior end and are very faint. The fossula is smooth and convex with as many as six denticles. Typically the shell is

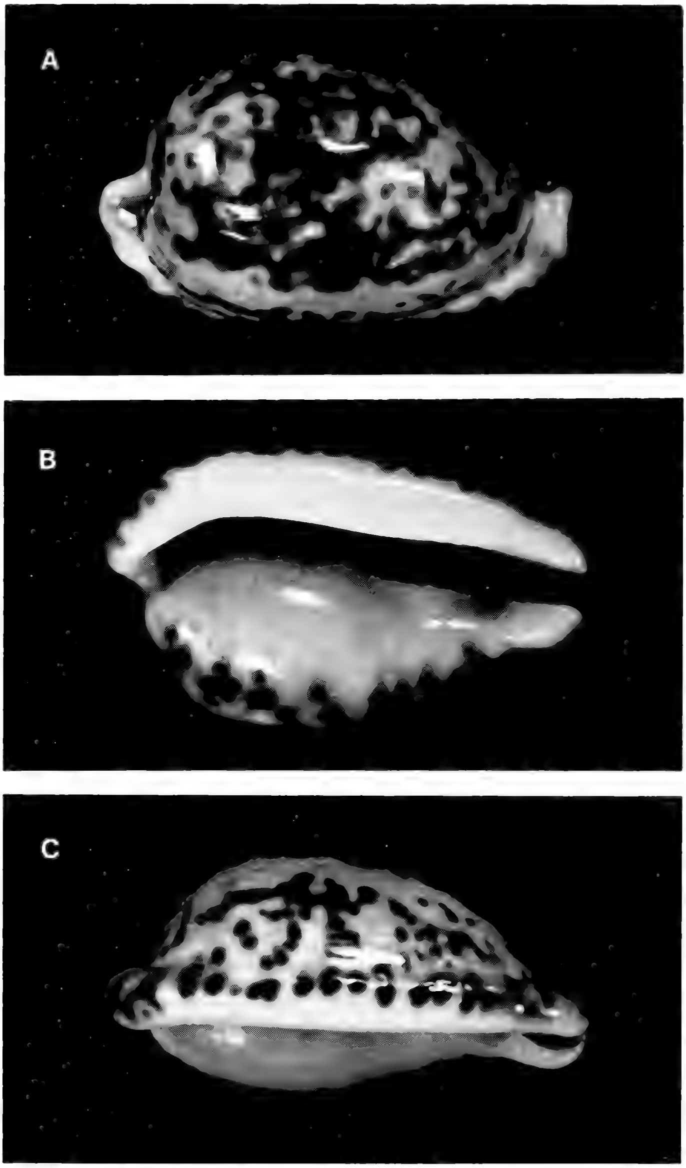

Fig. 21. *Cypraea edentula* Gray, 1825. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

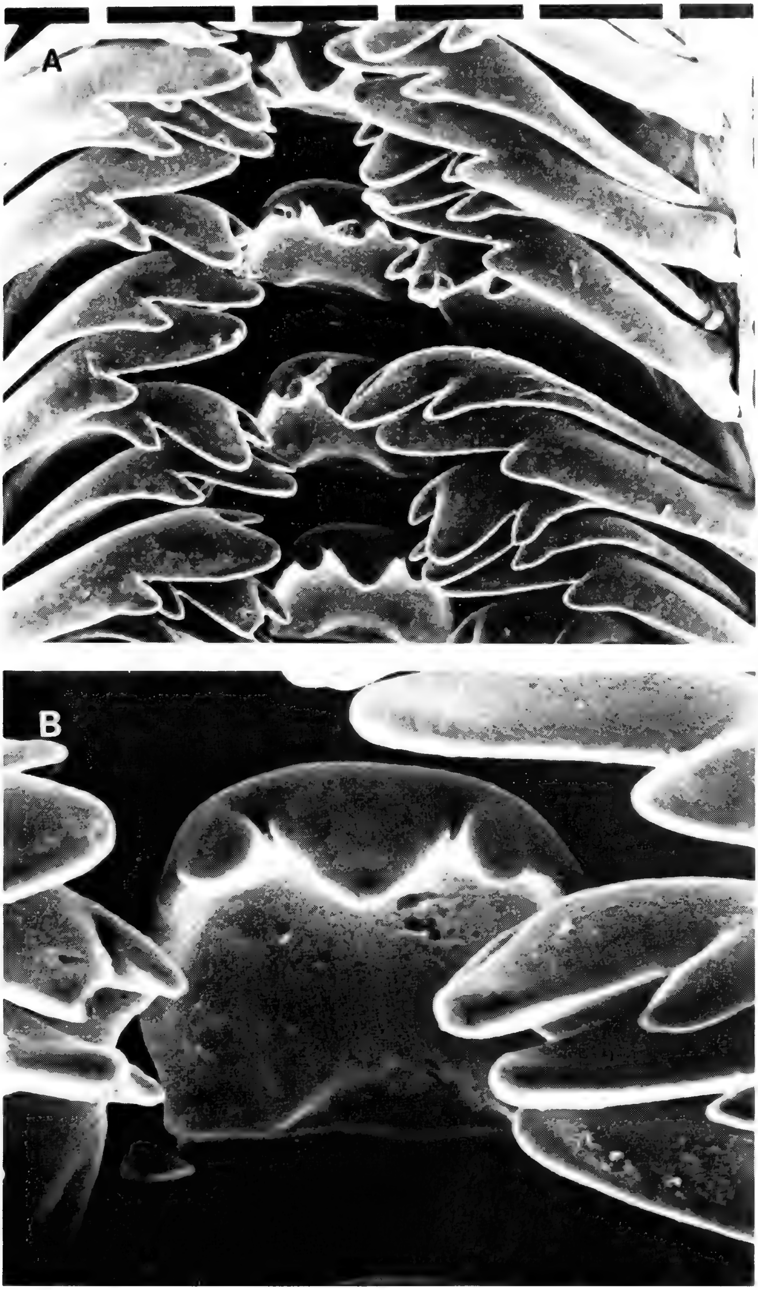

Fig. 22. *Cypraea edentula* Gray, 1825. Scanning electron micrographs of radula. A. Entire width. B. Central region.

thinly calcified with a brown or flesh ground-colour. Fulvous spots or blotches cover the dorsal surface. In some specimens, which are known as *C. edentula* var. *alfredensis* Schilder & Schilder, the shell is noticeably more heavily calcified. In these specimens the denticles tend to be more strongly developed on the labrum and the ground-colour of the shell is slate-grey. In all varieties the margins of the shell are white with brown spots. *Cypraea edentula* var. *alfredensis* may prove to represent a distinct species.

Living animal (Fig. 1G)

The foot is short and posteriorly rounded, the siphon is translucent white, strongly recurved and uneven at its tip. The tentacles are lemon-yellow to orange. They are slightly tapered and rounded at their tip. In one specimen the mantle was dark pink stippled with fine black spots. It had sparse whitish wart-like papillae, which were denser on the labral lobe than on the columellar lobe. On the columellar lobe were three large irregular protuberances. The second specimen had a lighter, more transparent mantle covered with dense green tomentose papillae. A few randomly spaced cabbage-like papillae were also present.

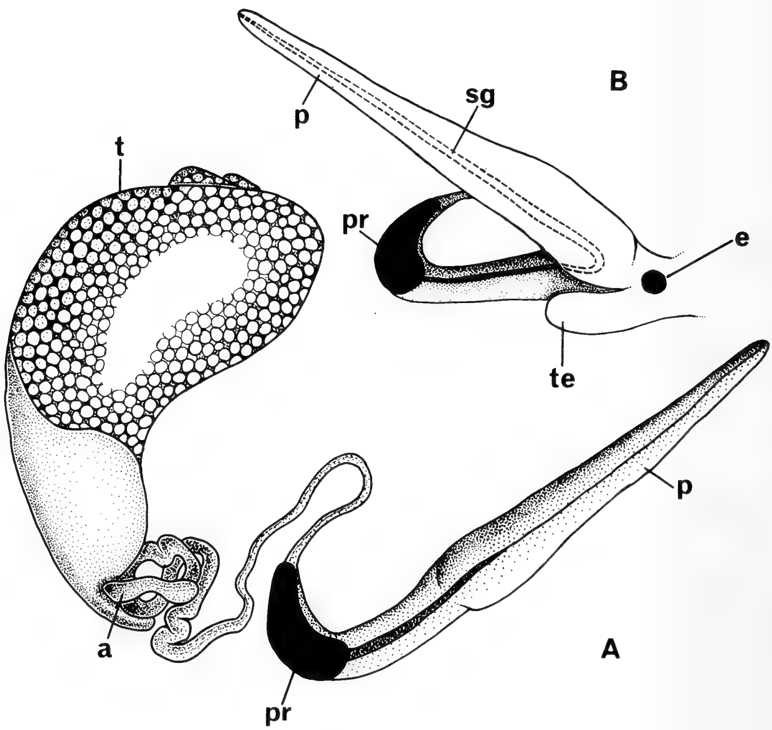

Fig. 23. *Cypraea edentula* Gray, 1825. A. Male reproductive system. B. Penis, opposite view.

Mantle complex

The arrangement of organs is identical to that described for *C. fuscorubra*. The hypobranchial gland is poorly preserved in the present material but the ctenidium consists of approximately 150 leaflets. The osphradium is triradiate.

Digestive system

The radular morphology is the only feature of the digestive system that differs from that of *C. fuscorubra*. The radular formula is $66 \times 3.1.3$ in one specimen. The rachidian teeth possess a rounded central cusp with round adjacent cusps (Figs 22, 33F). The base of the rachidian teeth is thin and centrally emarginate. The lateral teeth are broad and possess elongate central and adjacent cusps.

Central nervous system

The arrangement of ganglia is similar to that described for *C. fuscorubra* with a long pleural-subintestinal connective and elongate pedal ganglia.

Reproductive system

Only the male system has been studied (Fig. 23). There is a discrete prostate present at the posterior limit of the sperm groove, as in *C. algoensis*.

Cypraea cruickshanki Kilburn, 1972

Figs 24–27, 33G

Cypraea (Cypraeovula) cruickshanki Kilburn, 1972: 210, pl. 1, text-fig. 1.

Material

A single, freshly dead specimen (SAM–A35987) was collected by a commercial fishing trawler in about 800 m of water approximately 50 km east of Durban. Dead shells of other specimens in the private collections of several individuals were also examined.

Distribution

This species appears to be restricted to the coast of Natal in relatively deep water. It inhabits depths that exceed that of any other known species of *Cypraea*.

Shell (Fig. 24)

The shell is globose, 25,8–33 mm in length. The spire is umbilicate and calloused, covering the protoconch. The labrum is broad, widest centrally and is not glossy. The labrum possesses 20–22 coarse denticles that extend across one-half to three-quarters of the width of the labrum. The anteriormost and posteriormost labral teeth occasionally extend around the labrum, forming tubercles that are visible dorsally. A tubercle is always present on either side of the siphonal canal. The aperture is narrow, widest anteriorly. There are

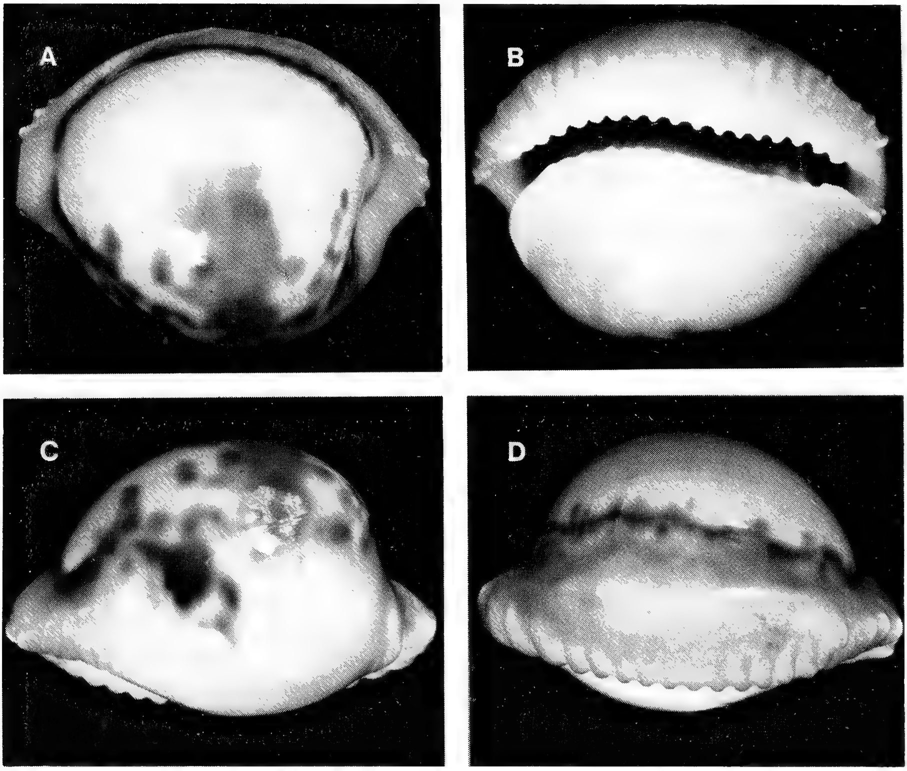

Fig. 24. *Cypraea cruickshanki* Kilburn, 1972. Shell (dorsally pigmented specimen). A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect (left). D. Lateral aspect (right).

18–21 columellar teeth, which are finer than the labral teeth. The fossula is well developed with 4–7 weak to strong denticles. The dorsum may be white, yellow or orange. Occasionally specimens may have brown dorsal spots or blotches.

Living animal

Although living specimens have not been observed, the freshly dead specimen examined in this study had a smooth mantle and foot that were whitish in colour. The slender tentacles were also white.

Mantle complex

The organs within the mantle cavity are arranged in the same manner as in *C. fuscorubra*.

Digestive system

The buccal mass, oesophagus, digestive gland and intestine are arranged in the same fashion as in *C. fuscorubra*. The radular formula is 76 × 3.1.3 in the single specimen examined. The rachidian tooth (Figs 25, 33G) is broad with a pair

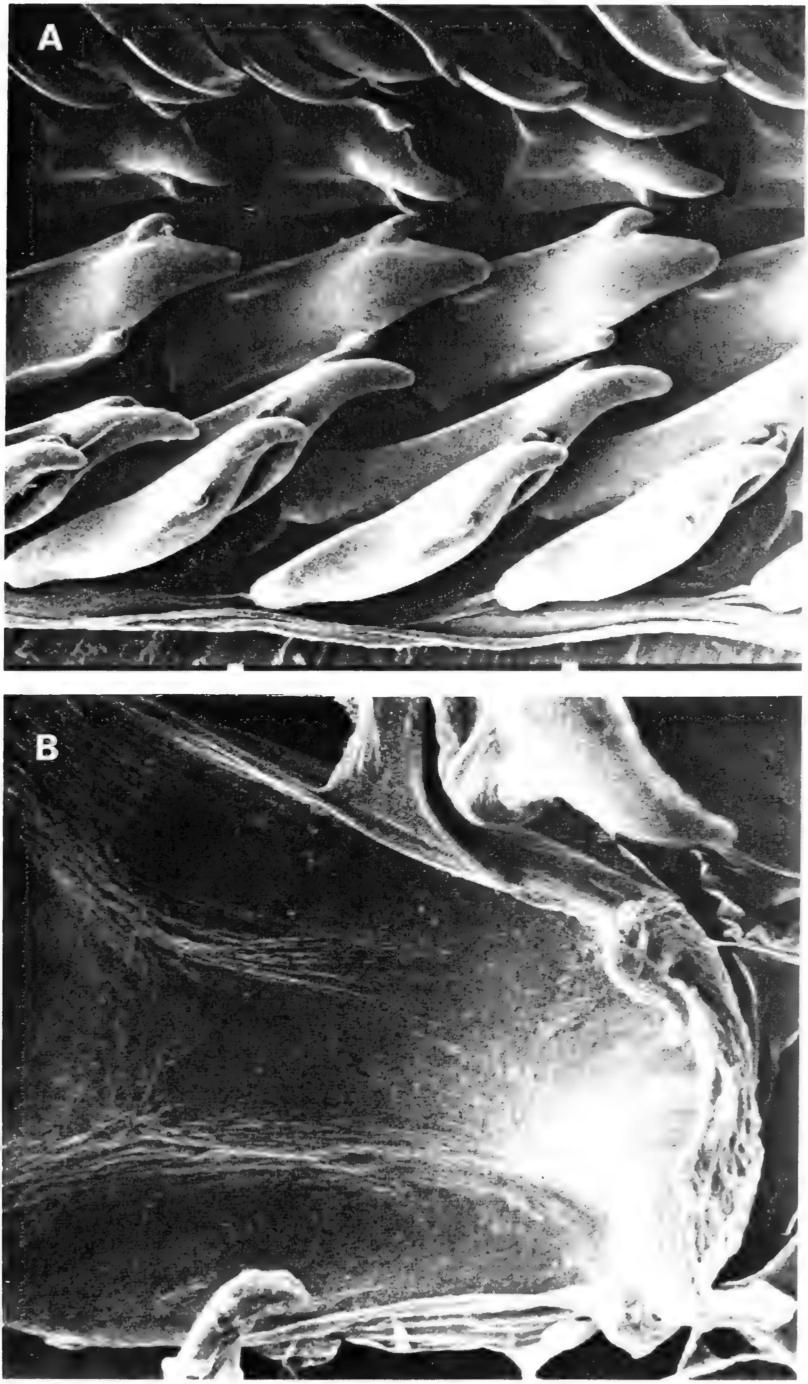

Fig. 25. *Cypraea cruickshanki* Kilburn, 1972. Scanning electron micrographs of radula. A. Entire width. B. Central region.

of ridges on either side of the centre of the tooth. The base of this tooth is well developed and centrally emarginate. On either side of the rounded central cusp is a round denticle. The central cusp and adjacent denticles are rounded on the inner lateral tooth and increase in length successively in the outer two laterals.

Central nervous system

The arrangement of ganglia is similar to that described for *C. fuscorubra* with the exception of the pedal ganglia. In *C. cruickshanki* (Fig. 26) the pedal ganglia are spherical with nerves extending from their posterior surface.

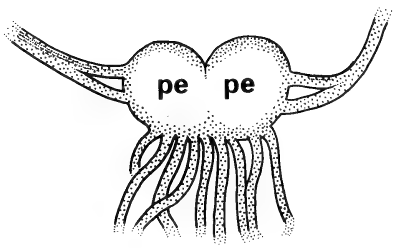

Fig. 26. *Cypraea cruickshanki* Kilburn, 1972.
Pedal ganglia.

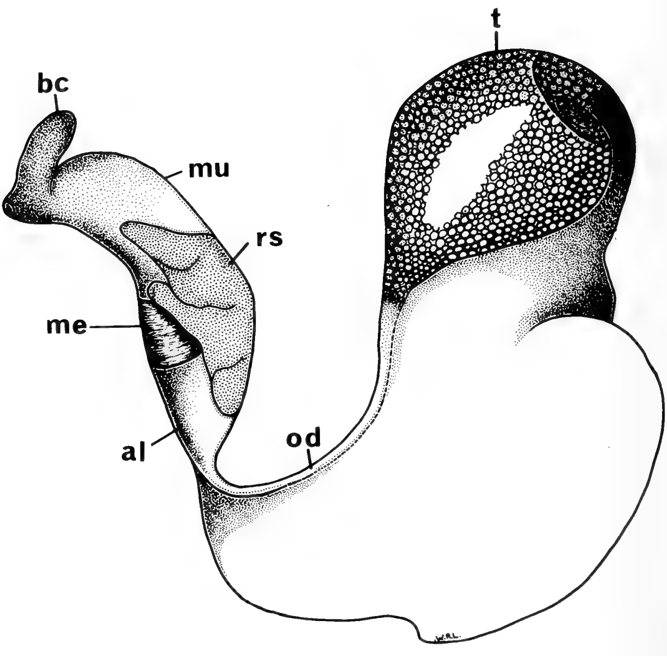

Fig. 27. *Cypraea cruickshanki* Kilburn, 1972. Female reproductive system.

Reproductive system

The single specimen available is a mature female (Fig. 27). The configuration of the reproductive organs is similar to that described for *C. fuscorubra*. However, the glandular receptaculum seminis of *C. cruickshanki* is less ramified than that of *C. fuscorubra*.

Cypraea iutsui (Shikama, 1974)

Figs 28–31, 33H

Cypraeovula (Crossia) iutsui Shikama, 1974: 24, fig. 2.

Material

The single preserved specimen (SAM–A35986), an immature female, was collected by the Department of Zoology of the University of Cape Town in 360–365 m of water off Cape Point.

Distribution

Specimens have been collected from the Olifants River mouth on the Atlantic coast of the Cape Province to the vicinity of Port Elizabeth, on the south-east coast.

Shell (Fig. 28)

The shell is globose, 23 to 38 mm in length. The spire is umbilicate and the protoconch is generally obscured. The labrum is rough in texture and not glossy. Its edge bears 17–25 fine teeth, which are generally white but occasionally are tinged with brown. These teeth extend across about one-quarter of the width of the labrum. The aperture is narrow and curved posteriorly. The columella possesses 12–23 teeth, which are strongest anteriorly. The fossula is poorly developed and generally lacks denticles. In one specimen three weak teeth are present on the fossula. The dorsal surface of the shell is pinkish with dense chestnut mottling. The basal callus is thin and white.

Living animal

The mantle surface is smooth off-white with fine irregular black dots.

Mantle complex

The arrangement of the organs within the mantle cavity is largely the same as in *C. fuscorubra*.

Digestive system

As in the preceding species the digestive system of *C. iutsui* is identical to that found in *C. fuscorubra*, with the exception of the radula. The radular formula is $80 \times 3.1.3$. The rachidian teeth are rectangular with a thickened central area and a strong slightly emarginate base (Figs 29, 33H). Their central cusp is

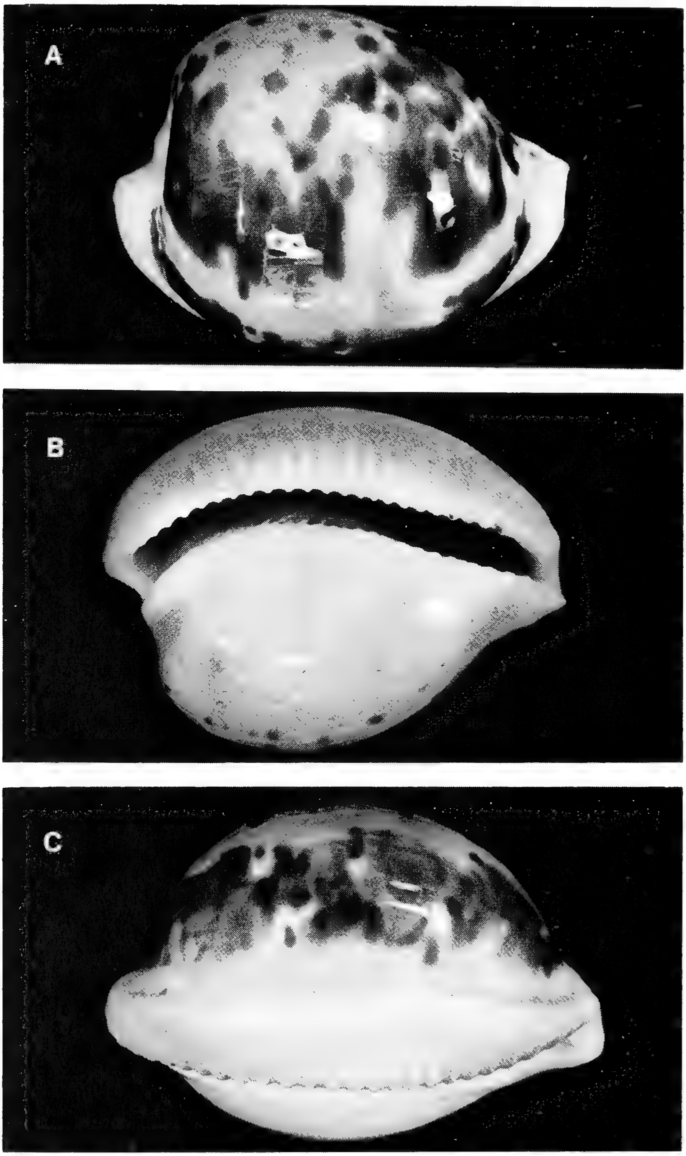

Fig. 28. *Cypraea iutsui* (Shikama, 1974). Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

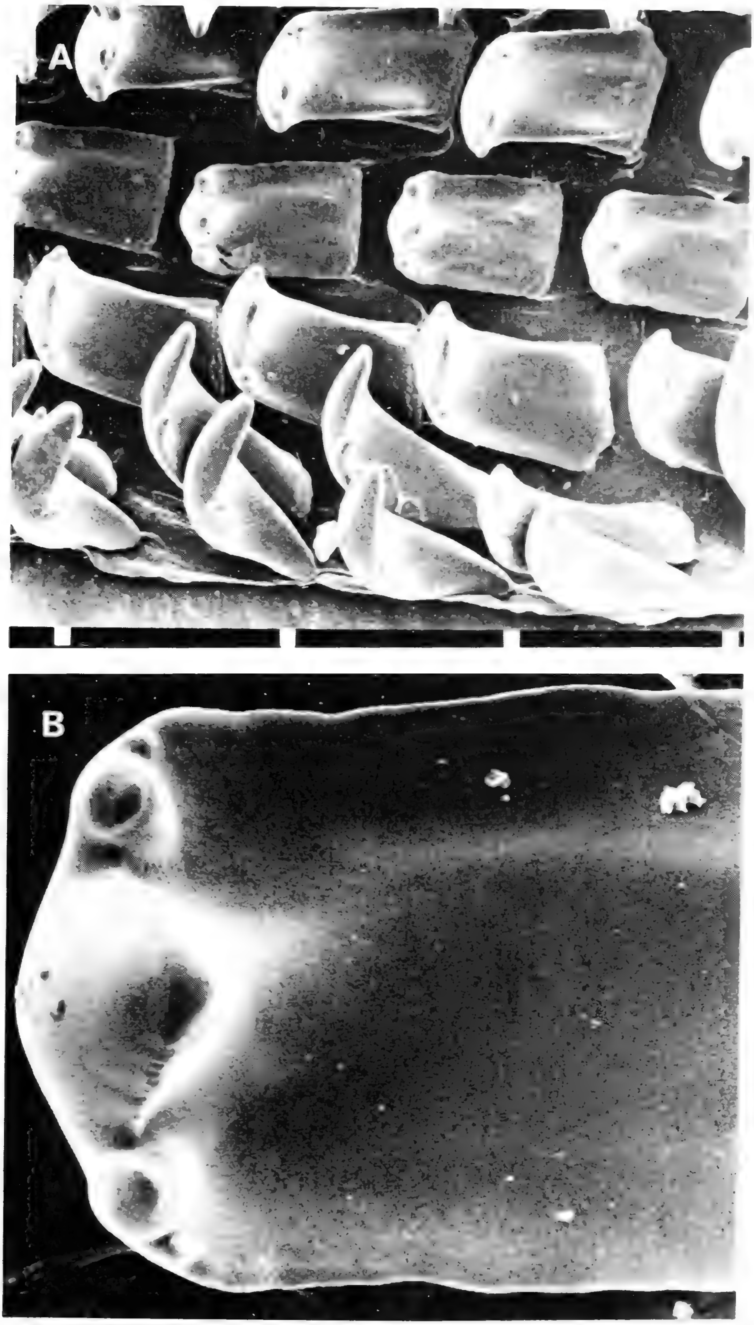

Fig. 29. *Cypraea iutsui* (Shikama, 1974). Scanning electron micrographs of radula. A. Entire width. B. Central region.

rounded, triangular with round lateral denticles. On either side of the lateral denticles is a rounded central cusp, as in *C. coronata*. The lateral denticles, unlike those of *C. coronata*, lack secondary denticles on their inner edge.

Central nervous system

The ganglia of *C. iutsui* differ in their arrangement from that described for *C. fuscorubra*. *Cypraea iutsui* is significantly more cephalized than any other of the South African endemic Cypraeidae. Most notably, the lateral nerve cord has been shortened so that the left pleural ganglion is immediately adjacent to the subintestinal ganglion (Fig. 30). As in *C. cruickshanki*, the pedal ganglia are spherical but there is only a single pair of nerves, which extend from the anterior rather than posterior end of the ganglia.

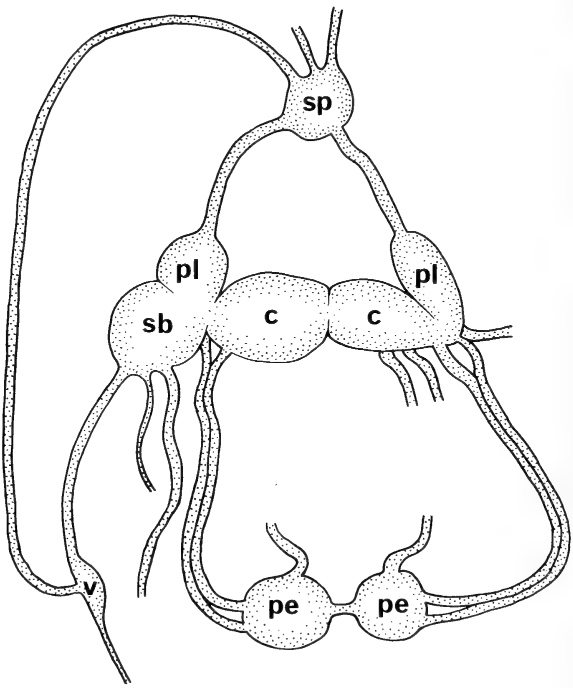

Fig. 30. *Cypraea iutsui* (Shikama, 1974).
Central nervous system.

Reproductive system

The single specimen is an immature female (Fig. 31). The oviduct has not yet undergone differentiation into the female gland mass and receptaculum seminis, although the bursa copulatrix is well developed.

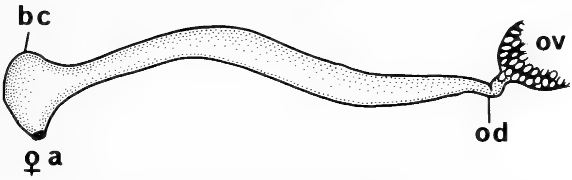

Fig. 31. *Cypraea iutsui* (Shikama, 1974). Immature female reproductive system.

BIOLOGICAL OBSERVATIONS

Ecology

The majority of known species of cowries are found in shallow tropical seas. Only a few species are known from temperate waters. *Cypraea spadicea* is known from cold waters of central and southern California. Only in southern Australia and South Africa are there large faunas of temperate endemics, consisting of more than ten species.

Eleven of the endemic South African cowries are limited to temperate waters, but four endemic species are restricted to the warm, subtropical waters of Natal.

The endemic cowries of southern Africa are unusual in that they are generally restricted to the sublittoral zone, the only exception being two specimens of *Cypraea capensis* that were found in the intertidal zone at Gonubie, near East London (Kilburn & Aiken 1972). Several species, *C. citrina, C. fuscorubra, C. fuscodentata, C. coronata, C. capensis, C. edentula* and *C. algoensis* are found in the sublittoral as shallow as 10–100 m depth, while *C. cruickshanki* and *C. iutsui* are known from depths of 400–800 m and 110–365 m, respectively. The depth distributions of *C. lisetae** and *C. fultoni* remain largely unknown as most specimens have been collected from fish stomachs.

Most cowries are known to prey on a variety of benthic algae and invertebrates including sponges, polychaetes and bryozoans, but little is known about their prey specificity. Hayes (1983) has recently demonstrated that the diet of some species of *Cypraea* may be restricted to a single species of sponge while others are far more generalized predators. *Cypraea coronata, C. fuscorubra, C. fuscodentata* and *C. algoensis* are often found in association with sponges. The intestine of the single specimen of *C. iutsui* examined in this study was full of sponge spicules, as were those of individuals of *C. edentula* and *C. fuscorubra*. *Cypraea coronata* has also been found together with bryozoans and polychaetes. Darkly pigmented specimens of *C. algoensis* from False Bay are usually found upon or adjacent to the crinoid *Comanthus wahlbergi*.

Developmental biology

Those tropical species of Cypraeidae of which the developmental patterns have been described possess a free-swimming veliger stage that metamorphoses

* See note on p. 122.

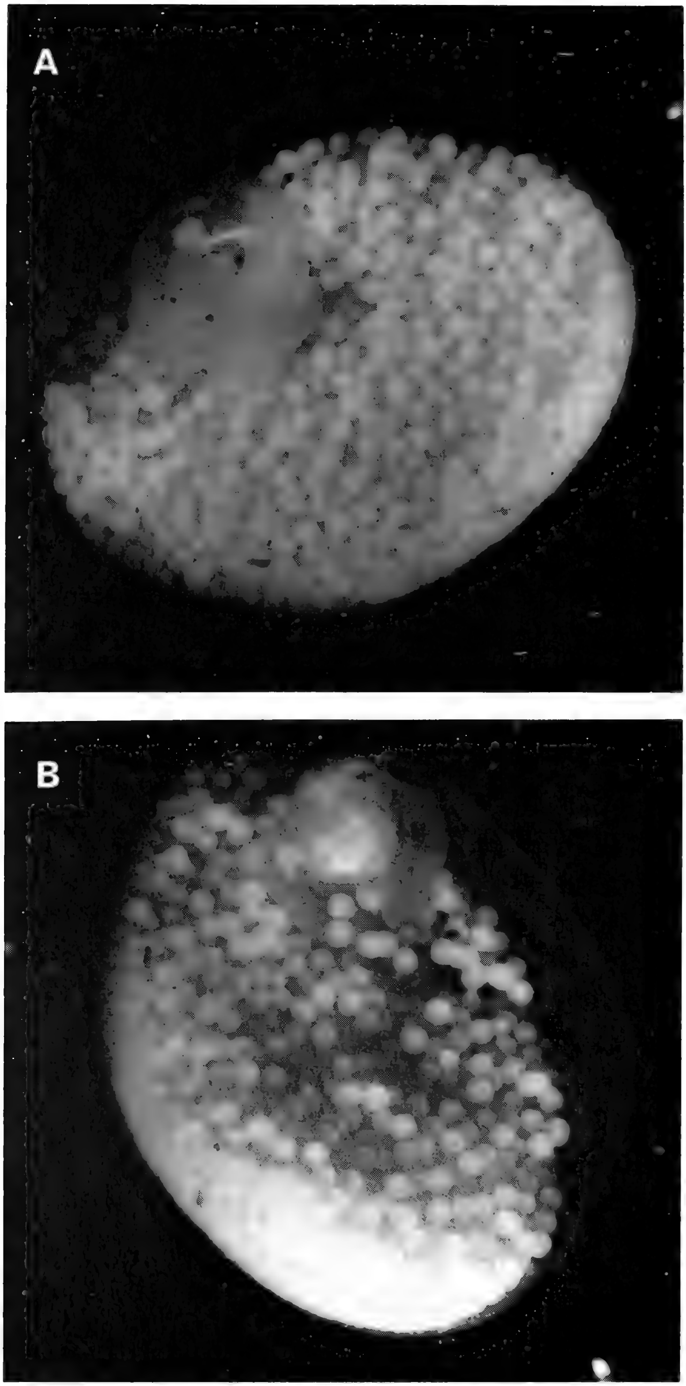

Fig. 32. *Cypraea algoensis* Gray, 1825. A–B. Developing embryos.

into a juvenile following a variable planktonic phase (Ostergaard 1950). Direct development has been observed in several species from southern Australia (Griffiths 1962) and in *Cypraea mus* from the northern coast of South America (Anonymous 1981). Kilburn & Rippey (1982) suggested that the cold-water endemics from southern Africa might exhibit direct development since the temperate Australian species demonstrate this pattern of development. In this study we have observed developing embryos of three species of endemic South African cowries, *C. algoensis, C. fuscodentata* and *C. fuscorubra*. These three species lack a free-swimming veliger stage and the post-metamorphic juvenile emerges directly from the egg capsule. The eggs are generally laid on the undersurface of rocks and are brooded by the female. One egg mass of *C. fuscodentata* consisted of 52 capsules with numerous white eggs. The capsules are 3,9 mm in diameter. The egg mass of *C. algoensis* consisted of 28 egg capsules, 3,8–4,0 mm in diameter, and contained whitish or yellow eggs. A single egg capsule was laid in a bucket of sea water by a freshly collected specimen of *C. fuscorubra*. It was similar in size and appearance to the capsules of the other two species. Developing embryos have been observed only in *C. algoensis*. The velum is greatly reduced but recognizable as a single ovoid lobe (Fig. 32). Juveniles have not been observed hatching from the egg capsules but well- developed embryos (Fig. 1H) have been observed with nurse eggs and were probably about ready to emerge from the egg capsules.

MORPHOLOGY OF *PEDICULARIA CALIFORNICA* NEWCOMB, 1864

Examination of specimens of *Pedicularia californica* Newcomb, 1864, in the course of this study, yields several interesting facts. The osphradium is triradiate with leaflets absent from the left margin (Fig. 34A). The pedal ganglia are spherical in shape without posteriorly directed extensions. The animals are gonochoric. The male system (Fig. 34B) consists of a highly convoluted ampulla, which gradually forms a short vas deferens. The tubular vas deferens terminates near the opening of the mantle cavity, where it empties into a ciliated sperm groove. The sperm groove continues along the right side of the body and along the ventral side of the penis. Kay (1957*a*) erroneously stated that *Pedicularia* has closed reproductive ducts. At the base of the penis is a dermal prostate gland that empties into its own ciliated groove and joins the sperm groove. The female system (Fig. 34C) is similar to that described by Ghiselin & Wilson (1966) for *Cyphoma gibbosum*, except that an ectal bursa copulatrix is absent.

GENERIC SUBDIVISION

The Cypraeidae represent a large family of gastropods with an extensive literature, primarily owing to their interest to shell collectors. Most of these works are strictly conchological or distributional in nature and few morphological

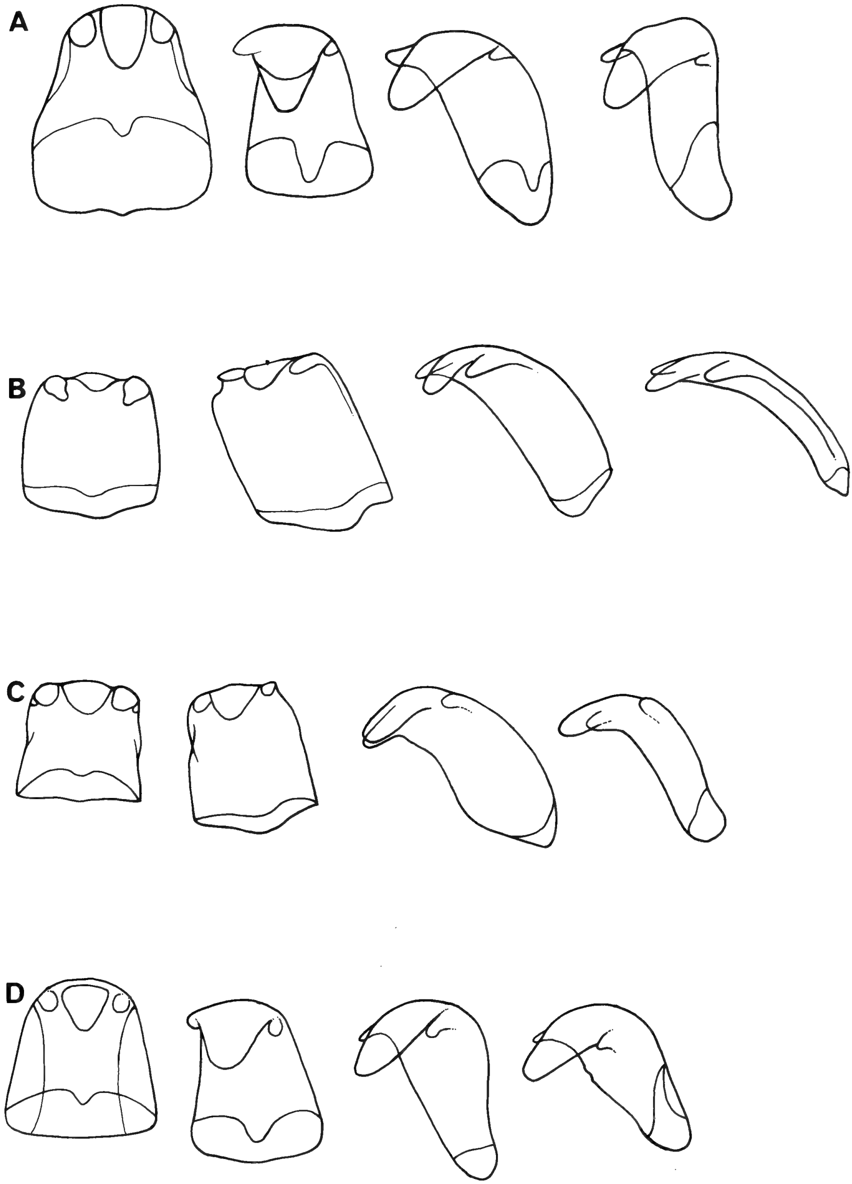

Fig. 33. Radulae of South African Cypraeidae. A. *Cypraea fuscorubra* Shaw, 1909. B. *Cypraea algoensis* Gray, 1825. C. *Cypraea coronata* (Schilder, 1930). D. *Cypraea fuscodentata* Gray, 1825.

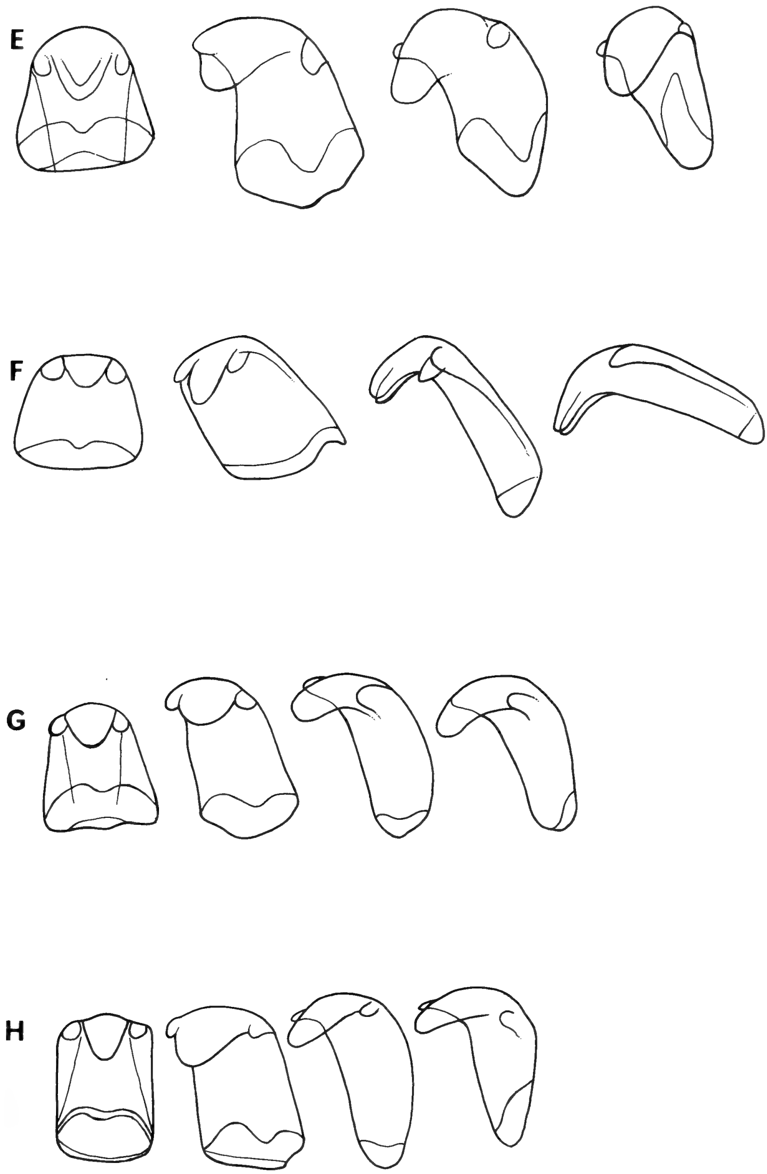

Fig. 33 *(continued)*. E. *Cypraea capensis* Gray, 1828. F. *Cypraea edentula* Gray, 1825. G. *Cypraea cruickshanki* Kilburn, 1972. H. *Cypraea iutsui* (Shikama, 1974).

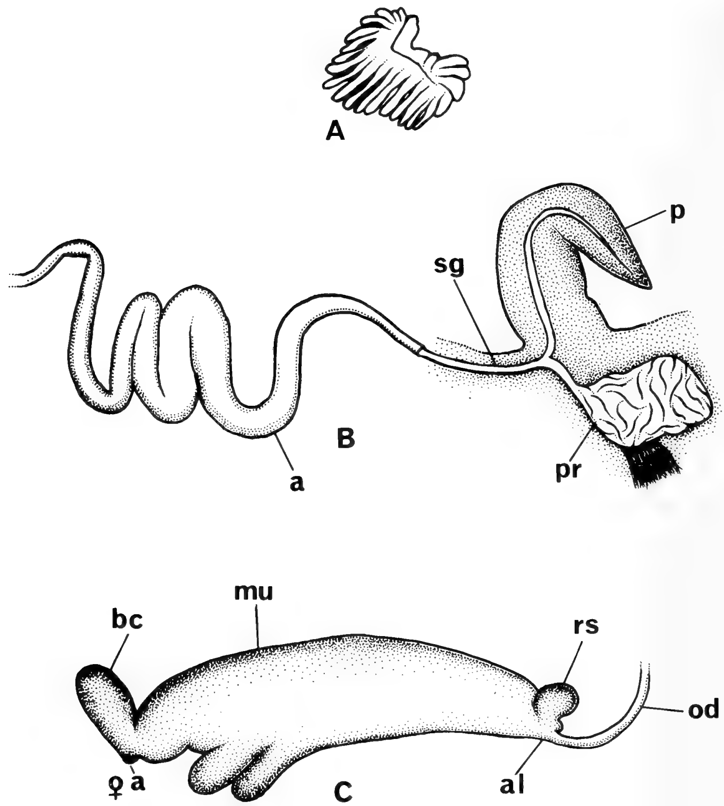

Fig. 34. *Pedicularia californica* Newcomb, 1864. A. Osphradium. B. Male reproductive system. C. Female reproductive system.

studies have been conducted (Shaw 1909; Vayssière 1923, 1927; Riese 1931; Rau 1934; Risbec 1937; Kay 1960*a*, 1960*b*, 1961, 1963). Wilson & McComb (1967) utilized subgeneric names within *Cypraea*. Kay (1960*a*: 283) stated that 'the species of *Cypraea* thus far examined are characterized by an extremely conservative anatomical picture'. However, she described considerable variability in the radula and female reproductive morphology, which had not previously been recorded. Recognition of these features resulted in species groups that differed from previous systems, which were based largely on conchological features. As the morphology of about only one-third of the described species was known, Kay (1960*a*) stated that it was better to include all members of the Cypraeidae in the single genus *Cypraea* until more comparative data became available. This was a dramatic departure from previous classifications (Schilder 1936; Steadman & Cotton 1946; Allan 1956), which subdivided the family into 24–61 genera. Subsequently, Cernohorsky (1965) incorporated many of the specific changes suggested by Kay (1960*a*), but divided the family into 28 genera.

A similar situation exists in the closely allied Triviidae. Cate (1979) subdivided the triviids into 15 genera based solely on conchological features. More recently, Gosliner & Liltved (1982) found considerable variation in internal morphology and suggested that all species be contained in the single genus *Trivia* until sufficient information was available to ascertain natural groupings. The fact that the present study demonstrates even greater morphological variability within the Cypraeidae supports Kay's contention that insufficient information is presently available to divide the family. The present study therefore maintains all species within the single genus *Cypraea*, until the morphology of the endemic Cypraeidae of southern Africa is more fully known.

MORPHOLOGICAL VARIABILITY

Great variability exists in the morphology of the shell. Despite claims by several workers that there is little morphological variability in the Cypraeidae, most organ systems vary considerably more than previously indicated. For this reason it is imperative to review the available morphological data.

Shell

The South African endemic cypraeids exhibit a propensity for sinistrality not found in other members of the family. Sinistral shells are rare, in any case, but have been found in specimens of *Cypraea edentula, C. fuscodentata* and *C. capensis*.

Mantle

Schilder (1936), Kay (1963), Cernohorsky (1965), and Wilson & McComb (1967) have suggested that the coloration and ornamentation of the mantle and siphon in living specimens are important criteria for distinguishing species. This is particularly true of the shape of the papillae. Schilder (1936) stated that closely allied species such as *C. staphylea* and *C. limacina* can be distinguished by their shells and living animals despite the fact that their radulae are very similar. The usefulness of mantle characteristics for the separation of species groups into higher taxa has been successfully employed (Kay 1963, 1981) but needs to be more fully explored.

Our observations of living representatives of these species from South Africa in the present study confirm Schilder's (1936) observations. Within the endemic South African Cypraeidae most species possess simple wart-like papillae. In *C. algoensis, C. fuscodentata* and *C. fuscorubra* the number and density of papillae are variable and they may often be entirely absent. The mantle of *C. coronata*, on the other hand, is always densely papillate with wart-like tubercles. In *C. edentula* cabbage-like papillae are present in addition to simple ones. The colour of the mantle varies intraspecifically. *Cypraea fuscorubra* exhibits the greatest variability in coloration while in *C. coronata* only the proportions of the various pigments vary. Despite the intraspecific variability of mantle colour most

South African endemic species can be distinguished on the basis of their mantle characteristics (Fig. 1).

Mantle complex

A certain degree of variability has been described for the mantle complex in the Cypraeidae. Schilder (1936) suggested that differences in elaboration of the osphradium and ctenidium might constitute a basis for the division of genera in the family. Kay (1960*a*) stated that such differences might be useful in separating closely related species but discounted their usefulness in separating genera. Later (1963) she noted that *C. testudinaria* and *C. hesitata* are unique in having a bifid rather than triradiate osphradium, but all other morphological features confirm that the species are not closely related. From this study it is apparent that there is little variation in the morphology of the mantle complex between species of endemic South African cypraeids.

Digestive system

The morphology of the digestive system of *Cypraea* has been studied by Rau (1934), Risbec (1937), and Kay (1960*b*). Minor interspecific differences have been noted in the elaboration of the salivary glands, stomach and buccal mass (Risbec 1937) but their intraspecific variability has not been fully determined. Therefore the systematic value of these characters remains open to question.

There is little variation in the gross morphology of the digestive system in the species examined in this study, and the pattern agrees with that described by Rau (1934, fig. 43) and Kay (1960*b*) with the exception that the salivary glands are largely fused into a single mass.

Most of the variation in the digestive system has been focused on the morphology of the radular teeth. Kay (1960*a*) described four basic radular types. The majority of species are known to possess a 'R1' radula with dumb-bell shaped internal bracts at the base of the rectangular rachidian tooth. Within this radular 'type' there seem to be several major variants. The presence or absence of basal denticles on the rachidian and inner lateral teeth and the subtending bract at the base of the rachidian appear to be species-specific. Kilburn & Aiken (1972) noted that the radula of *C. fultoni* lacked a subtending bract and denticles and compared its radula to that of *C. rosselli* (Wilson & McComb 1967). The same morphological pattern is found in the radulae of all of the other South African endemics examined in this study. No species studied had either subtending bracts or basal denticles. The radular teeth of *C. edentula* and *C. algoensis* appear to be significantly broader than those of any cypraeids with a 'R1' radula and differ markedly from those of other South African species (Fig. 33). Kay (1960*a*) stated that in *Cypraea* the radular teeth generally possess a single denticle on either side of the central cusp. Kilburn & Aiken (1972) noted that in the specimen of *C. fultoni* that they examined, there is a smaller secondary denticle on the outer side of the primary cusp and questioned whether this is characteristic of the species. Secondary denticles have also been described in several other species (Vayssière

1923, 1927; Risbec 1934). In the single specimen of *C. iutsui* examined in this study, secondary denticles are present on the rachidian tooth although they were not indicated by Barnard (1963, fig. 5C, as *C. fuscorubra* 'globose form'). Secondary denticles on the rachidian teeth and on the inner side of the inner laterals are characteristic of all specimens of *C. coronata* examined in this study (Fig. 13B).

A great deal more information is required to determine the range of variability within and between species of *Cypraea* to ascertain the systematic significance of the observed radular differences.

Central nervous system

The central nervous system in the Cypraeidae is highly modified from that of less specialized mesogastropods such as *Littorina* (Fretter & Graham 1962). The lateral nerve cords do not cross each other and are largely euthyneurous. A short zygoneurous connective links the left pleural and supraintestinal ganglia. There does not appear to be a zygoneurous connection between the right pleural ganglion and the subintestinal ganglion, although a thin connective was indicated by Riese (1931).

Shaw (1909) differentiated *Trivia* from *Cypraea* on the basis of the shape of the pedal ganglia: elongate in *Cypraea* and spherical in *Trivia*. This has served as a major criterion for separating the Cypraeacea from the Lamellariacea (Schilder 1936). Since Shaw's (1909) work all three subsequent studies of the nervous system of the Cypraeidae (Riese 1931; Risbec 1937; Kay 1957*b*) have confirmed the presence of elongate pedal ganglia within the family. Specimens of *C. fuscorubra, C. fuscodentata, C. coronata, C. algoensis, C. edentula* and *C. capensis* examined in this study had elongate pedal ganglia (Fig. 7). However, the ganglia of *C. iutsui* and *C. cruickshanki* are spherical as described for the Lamellariacea. In *C. cruickshanki* there are several elongate nerves emanating from the posterior ends of the ganglia (Fig. 26), while in *C. iutsui* a single pair of nerves extends anteriorly (Fig. 30).

Most authorities have stated that there is very little variability within the nervous system in the Cypraeidae. In addition to the differences already noted in the pedal ganglia, the length of the lateral nerve cord between the left pleural and subintestinal ganglia varies considerably between species. Risbec (1937) demonstrated that in species from New Caledonia this nerve cord is elongate in *C. arabica, C. lynx, C. tigris* and *C. carneola*, and short in *C. clandestina, C. moneta, C. annulus* and *C. erosa*. In *C. staphylea* the subintestinal ganglion is immediately adjacent to the left pleural ganglion. In all of the South African cowries examined in this study the lateral cord is elongate, with the exception of *C. iutsui*, in which the pleural and subintestinal are adjacent as in *C. staphylea*.

Risbec (1937) also noted that a variable number of accessory ganglia are present along the lateral nerve cords in the various *Cypraea* species he studied. Some species, such as *C. clandestina*, have only a single accessory ganglion. *Cypraea erosa, C. moneta, C. errones* and *C. annulus* possess two ganglia;

C. staphylea and *C. carneola* three, *C. arabica* four, and *C. tigris* seven. All the South African species examined have only a single accessory ganglion present between the supraintestinal and visceral ganglia, as in *C. staphylea*.

Reproductive system

Kay (1960*a*) described two basic forms of the female reproductive system of the Cypraeidae: in the first instance a bursa copulatrix is present and also a glandular receptaculum seminis, which is granular in texture; in the second form a bursa is absent but a saccate receptaculum is present. Kay (1963) described interspecific morphological variability in the shape of the bursa copulatrix. Kilburn & Aiken (1972) stated that in the reproductive system of *C. capensis* a bursa is present and the receptaculum is apparently glandular. All of the six species of South African Cypraeidae in which the female reproductive system was examined in this study, possess a bursa copulatrix and a saccate, diverticulate receptaculum seminis. In each instance the bursa is simply saccate as described from *C. argus* (Kay 1963, fig. 6a). The receptaculum, although saccate, appears to have a glandular epithelium, but this needs to be verified by means of histological examination. The fact that all South African endemic species thus far examined (with the possible exception of *C. capensis*, which needs to be re-examined) possess both a saccate receptaculum and a bursa further suggests that the structure of the female reproductive system is likely to be systematically significant.

Little variation has been described in the male system of the Cypraeidae. There appear to be only minor differences in the shape of the penis (Kay 1960*a*). All of the South African species examined possess a simple conical penis with a ventral sperm groove extending to its tip as described by Kay (1960*b*). The prostate in *Cypraea* has been described as an elongate, club-shaped or rectangular structure (Kay 1960*a*). Wilson & McComb (1967) described some variation in the shape and size of the prostate. In the South African Cypraeidae there are two types of prostate glands. In *C. fuscodentata, C. fuscorubra* and *C. coronata* a distinct prostate is absent and the walls of the sperm groove are lined with glandular cells (Fig. 8B). In *C. edentula* and *C. algoensis* a discrete prostatic region is situated at the ental end of the sperm groove (Figs 11B, 23).

SYSTEMATICS OF ENDEMIC SOUTH AFRICAN CYPRAEIDAE

The taxonomy of the endemic Cypraeidae of southern Africa has historically been a source of considerable confusion, and this situation persists. The precise number of constituent taxa cannot be accurately determined at present. Until now the majority of species have been known only from beach-worn shells. While many questions remain unanswered, the information presented in this study does permit some of the systematic controversy to be resolved.

The endemic Cypraeidae of South Africa consist of several major components. *Cypraea citrina* Gray, 1825, is found from the coast of Mozambique

to Jeffreys Bay in the eastern Cape Province. It appears to be closely allied to the widespread Indo-Pacific species *C. helvola* and *C. marginalis*, although nothing is known about its internal morphology. *Cypraea lisetae* Kilburn, 1975,* is conchologically most similar to *C. midwayensis*, which was designated as the type species of *Nesiocypraea* Azuma & Kurohara, 1967, because of the unique shape of the rachidian teeth. Unfortunately the radula of *C. lisetae* remains unknown. *Cypraea fultoni* Sowerby, 1903, has been placed in *Bernaya* and appears to be allied to several species that are restricted to south-western Australia (Schilder 1936).

The remaining endemic species have been placed in the genera *Luponia* and *Cypraeovula* (Schilder 1936), which appear to be restricted to southern Africa but may be allied to the south-western Australian endemics. Within these taxa there appear to be three species complexes, which can be recognized conchologically and by their internal morphology. The first group consists of *Cypraea cruickshanki* Kilburn, 1972, and *C. iutsui* (Shikama, 1974). The status of these species has been the subject of much debate. When Kilburn described *C. cruickshanki* he also included photographs and a discussion of several specimens that Barnard (1963) had previously considered as a globose form of *C. fuscorubra* Shaw. Kilburn contended that this form appeared to be distinct from *C. fuscorubra* and was similar to *C. cruickshanki*, but insufficient material prevented a detailed comparison. Shikama (1974) described *Cypraeovula iutsui* based on a single specimen collected from southern Africa. Burgess (1977) suggested that *Cypraea iutsui* is merely the fully mature stage of *C. cruickshanki*. Kilburn & Rippey (1982) recently stated that *C. iutsui* is either a cold-water form of *C. cruickshanki* or a deep-water form of *C. fuscorubra*. Examination of preserved animals and shells in this study confirms that *C. iutsui* is distinct from both *C. cruickshanki* and *C. fuscorubra*. The conchological features distinguishing *C. iutsui* (as *C. fuscorubra* globose form) from *C. cruickshanki* described by Kilburn (1972: 214, table II) are consistent with material examined in this study. The most obvious difference between the two is the prominent versus fine labral teeth of *C. cruickshanki*, which traverse most of the width of the labrum. The fossula of *C. cruickshanki* is prominent with 4–6 denticles while in *C. iutsui* it is poorly developed with no or, more rarely, three denticles. In *C. iutsui* the posterior limit of the labrum extends beyond the body whorl while in *C. cruickshanki* they are approximately the same length. In *C. cruickshanki* the anterior and posterior columellar teeth extend on to the columella while in *C. iutsui* they do not.

The internal differences between the two species are even more profound. The rachidian teeth of *C. cruickshanki* have a narrow raised portion while in *C. iutsui* this area is much wider (Figs 29, 33). *Cypraea iutsui* has small accessory denticles on the outer side of the rachidian tooth, which are absent in *C. cruickshanki*. The most significant morphological differences are present in the central nervous system. In *C. iutsui* the subintestinal ganglion is immediately

* See note on p. 122.

adjacent to the left pleural ganglion while in *C. cruickshanki* they are separated by a moderately long nerve cord. The nerves emanating from the pedal ganglia are anteriorly directed in *C. iutsui* and posteriorly directed in *C. cruickshanki*. The two species appear to be entirely geographically isolated, as well.

Burgess (1977) suggested that *C. cruickshanki* should probably be placed in a separate genus based on its conchological uniqueness. The fact that *C. cruickshanki* and *C. iutsui* are the only cypraeids known to possess spherical pedal ganglia adds credence to this idea. However, more information concerning the range of variability of this character within the Cypraeidae is required to establish generic or subgeneric limits.

The second major group of endemic cypraeids includes *Cypraea algoensis* Gray, 1825, and *C. edentula* Gray, 1825. Conchologically these two species are pyriform to globular. In both cases the margin of the shell is ornamented with dark purple or brown spots. These taxa share certain internal features that are absent from other South African cypraeids. The radular teeth are significantly broader than in other species and a discrete prostate gland is present. These characteristics may justify the placement of these taxa within the distinct subgenus *Luponia* Broderip, 1837. *Cypraea edentula* and *C. algoensis* can be distinguished by several conchological and morphological features. *Cypraea edentula* generally lacks labral or columellar teeth, but rudiments may occasionally appear on the labrum. *Cypraea algoensis* possesses fine but well-developed teeth on the labrum and columella. In *C. edentula* the fossula is well developed and strongly denticulate while it is poorly developed with occasional denticles in *C. algoensis*. There appear to be slight but consistent radular differences between the two species. The central and adjacent cusps of the rachidian teeth are rounded in *C. edentula* and elongate in *C. algoensis*. There do not appear to be any significant differences in the nervous and reproductive systems. The two species are geographically isolated; *C. edentula* is known from Tsitsikama Coastal National Park to the south-western Transkei, while *C. algoensis* has been found from the Atlantic coast of the Cape Peninsula to Cape Agulhas.

The largest number of endemics are contained within the third group. The constituent species of this group have been the subject of considerable systematic confusion and disagreement. Unfortunately the morphology of several of these taxa remains largely unknown. All authorities who have studied the South African Cypraeidae agree that *Cypraea fuscodentata* Gray, 1825, *C. fuscorubra* Shaw, 1909, and *C. capensis* Gray, 1828, represent distinct valid species. Beyond this, there is little agreement about the systematics of the remaining taxa.

Much of the controversy surrounding this group relates to a pair of species that have been confused, synonymized, or renamed owing to homonymy. A detailed historical account of the problems is provided by Burgess (1982). Briefly, *Cypraea similis* Gray, 1831, was found to be a junior homonym of *C. similis* Gmelin, 1791 (= *C. erosa* Linnaeus, 1758). Later, *Cypraea castanea* Higgins, 1868, was discovered to be a junior homonym of *C. castanea* Röding, 1798. Shaw (1909) noted this problem and considered Gray's and Higgins' species as

subjective synonyms. He provided *C. fuscorubra* as a new name for *Cypraea similis* Gray and designated Gray's specimen as the holotype of *C. fuscorubra*. Burgess (1970) recognized that there were conchological differences distinguishing Gray's and Higgins' material but erroneously provided a new name for Gray's rather than Higgins' material. Thus *C. gondwanalandensis* became a junior objective synonym of *C. fuscorubra* Shaw (Kilburn 1972). This error was corrected by Burgess (1982): he named *C. verhoefi* based on Higgins' holotype of *C. castanea*. Kilburn & Rippey (1982) considered *C. verhoefi* (as *C. castanea*) as a junior subjective synonym of *C. fuscorubra* despite the significant conchological differences discussed by Burgess (1970, 1982). No preserved animals of *C. verhoefi* have been examined, nor are any presently available. A definitive statement concerning the taxonomic status cannot be made until the morphology of *C. verhoefi* is known, but the consistent conchological differences between them strongly suggest that Burgess is correct in maintaining their separation.

Cypraea coronata (Schilder, 1930), which is normally characterized by having tubercles around the outer margin of the shell, has not been reported in the literature since its original description. Kilburn & Rippey (1982: 62) considered it as an 'interesting form of *C. fuscodentata*'. There are several conchological characters separating *C. fuscodentata* and *C. coronata*. The presence of tubercles and the slightly irregular outline of *C. coronata* most clearly distinguish it from *C. fuscodentata*. The columellar teeth of *C. fuscodentata* are dark brown and the majority cover most of the width of the columella. In *C. coronata* the teeth are white or light brown and normally only the anteriormost and posteriormost teeth extend beyond the aperture on to the columella. The form of the radular teeth also clearly differentiates the two. *Cypraea coronata* has accessory denticles on the outer edges of the rachidian and inner lateral teeth, which are absent in *C. fuscodentata*. These differences in conchology, internal morphology and appearance of the living animal (Fig. 1) distinguish *C. coronata* as a distinct species.

Cypraea gloriosa (Shikama, 1971) was originally thought to have been collected from the South China Sea. Burgess (1977) and Kilburn & Rippey (1982) have pointed out that it is likely that it was collected off South Africa and consider it synonymous with previously described South African species. However, Burgess considered *C. gloriosa* as a junior synonym of *C. fuscodentata* while Kilburn & Rippey regarded it as a junior synonym of *C. fuscorubra*. The strong dentition of the columellar teeth extending on to the columella is more similar to that found in *C. fuscodentata*. However, the mottled coloration and large tubercles on the margins of the shell indicate that it should be regarded as a junior synonym of *C. coronata*.

The existence of two other taxa has recently been explained as the product of hybridization of well-defined species (Kilburn & Rippey 1982). *Cypraea cohenae* Burgess, 1965, is conchologically intermediate between *C. edentula* and *C. fuscodentata* while *C. amphitales* Melvill, 1888, is similar to *C. capensis* and *C. fuscodentata*. While the conchological intermediacy of these taxa could possibly be explained by hybridization there are no internal morphological or

biological data to support this claim. Detailed observation and examination of living and preserved specimens are required before definitive conclusions can be drawn. The fact that shells of *C. cohenae* are rare and are known only from a very limited geographical area (Jeffreys Bay) does not preclude that they may be relatively common and widespread in the sublittoral. Shells of several cypraeids are rarely found on the beaches of the Cape Peninsula but are fairly commonly found in the shallow sublittoral. If indeed *C. edentula* does interbreed with *C. capensis* and *C. fuscodentata* it would certainly reduce the systematic importance of the radular and prostatic differences between representatives of these species groups.

HIGHER SYSTEMATICS AND PHYLOGENY OF THE CYPRAEACEA AND LAMELLARIACEA

The higher systematics of the Cypraeacea and Lamellariacea within the Mesogastropoda has been the subject of considerable disagreement and confusion. In some cases even the same author has produced several conflicting schemes of classification (Schilder 1936, 1966, 1969).

Much of the argument concerning the classification of these two superfamilies relates directly to the position of the Triviidae (including Eratoinae). Conchologically most triviids appear to be closely allied to the Cypraeidae and Ovulidae and have traditionally been classified with them (Shaw 1909). The discovery of the fact that the Triviidae and Lamellariidae possess a double-shelled larva called an echinospira led Schilder (1936) to suggest that the Triviidae are more closely allied to the Lamellariidae than to the Cypraeidae and Ovulidae. The observation that an echinospira larva is also present in *Capulus ungaricus* (Lebour 1937) further complicated the problem, as the capulids have been considered to be closely allied to the Calyptraeidae and Trichotropidae. On the bases of conchological and larval features Fretter & Graham (1962) stated that the Cypraeacea, Lamellariacea and Calyptracea are all closely allied, and maintained the placement of the Triviidae in the Lamellariacea. More recently, Schilder (1966) altered his opinion and suggested that the Triviidae are more closely related to the Cypraeacea, as did Kay (1960*b*). Speculation with regard to these mesogastropods has significantly exceeded the collection and careful analysis of data. In some cases the examination of one or two species has been employed to characterize an entire family. This has led to erroneous assumptions about morphological variability and its systematic significance. For example, it has been assumed since the work of Shaw (1909) that the Triviidae and Cypraeidae can be separated by the shape of the pedal ganglia. This is shown here to be incorrect as both configurations have been found in the South African Cypraeidae. The degree of morphological variability observed in the Cypraeidae in the present study and previously in the Triviidae (Gosliner & Liltved 1982) attests to the need for the accumulation of more detailed morphological data.

Another major problem in determining phylogeny is the establishment of the direction of evolutionary change. Kay (1960*b*) described differences of opinion as

to whether the elongate pedal ganglia found in most Cypraeidae are primitive or advanced features. None of the arguments put forth as to the ancestral state of the ganglia consider that more primitive mesogastropods such as *Viviparus* possess elongate pedal ganglia, and all ignore the fact that cephalization, or the concentration of nervous tissue into the cephalic region, is one of the most widespread evolutionary trends in the animal kingdom.

Consideration of the distribution of characters within other taxa and their functional significance generally permits one to make a reasonable estimate of the polarity of most characters. The trend to modify an open ciliated sperm groove to a closed tubular vas deferens is widespread throughout the Gastropoda (Kay 1960*b*). Ghiselin (1966) described the functional adaptive significance of this modification in opisthobranchs, while Morton (1955) and Fretter & Graham (1962) have demonstrated the same trend in pulmonates and neogastropods. Gosliner (1981) indicated that the most primitive living mesogastropods are probably littorinaceans and that they possess a sperm groove.

Ghiselin (1966) stated that the most primitive opisthobranchs probably had an ental receptaculum seminis and an ectal bursa copulatrix. This also appears to be the ancestral (plesiomorphic) state of the Pulmonata, Mesogastropoda (Gosliner 1981; Ghiselin & Wilson 1966) and Neogastropoda (Fretter & Graham 1962).

The larval stage of the vast majority of gastropods is a simple veliger. The presence of an echinospira larva in the Triviidae, Lamellariidae and Capulidae most likely represents a secondary modification of the veliger to facilitate flotation in taxa with a prolonged larval life (Fretter & Graham 1962). The question that remains is whether the presence of an echinospira in the Capulidae represents an independent acquisition of this larval type or implies phyletic proximity to the lamellariids and triviids. Adequate morphological information is not presently available to compare the Capulidae with the other taxa.

The osphradium is the primary chemosensory organ in the majority of prosobranch gastropods. In most mesogastropods it is a simple linear structure, but in the Triviidae, Lamellariidae, Naticidae and Neogastropoda it is foliate and bipectinate. This is usually correlated with the development of the siphon and increased predatory capabilities. In the Cypraeidae and Ovulidae, which also possess a siphon, the osphradium is well developed, but is triangular in shape (except where it is secondarily modified in *Cypraea hesitata* and *C. testudinaria* (Kay 1963)). Both the bipectinate and triangular osphradia of these taxa appear to be derived (apomorphic) from a simple linear ridge.

The most primitive mesogastropods such as *Littorina* are generalized grazing omnivores. Many members of the Cypraeidae appear to adopt this mode of feeding (Kay 1960*b*) but others are specialized carnivores (Hayes 1983). The majority of ovulids are specialized predators on alcyonaceans, except for *Pedicularia*, which feeds exclusively on stylasterine hydrozoan corals. The Triviidae and Lamellariidae feed upon, and lay their eggs within, tunicate colonies (Fretter & Graham 1962).

The determination of phylogenetic relationships of taxa may only be based upon shared derived characters (synapomorphies) (Hennig 1966). A comparison of the apomorphies present in the Triviidae, Lamellariidae, Ovulidae and Cypraeidae yields a clear picture of dichotomy between the Cypraeacea and Lamellariacea (Table 1, Fig. 35). The possession of a closed sperm groove, echinospira larva and large bipectinate osphradium unite the Triviidae and Lamellariidae. The morphological synapomorphies shared by the Lamellariidae and Triviidae are largely independent of their ecological association with compound tunicates, reducing the possibility that these similarities are due to parallelism. A triangular osphradium appears to be a uniquely derived character uniting the Ovulidae and Cypraeidae. The feeding specializations of the Ovulidae and associated radular modifications distinguish them from the Cypraeidae. The fused jaws of the Lamellariidae appear to be a modification of the distinct jaws of the Triviidae. Based on the above apomorphic characteristics placement of the Triviidae with the Lamellariidae seems to be the more compatible phylogenetic hypothesis.

TABLE 1

Morphology of the Cypraeacea and Lamellariacea.

Character	Triviidae	Lamellariidae	Ovulidae	Cypraeidae
1. vas deferens	d—closed	d—closed	a—open	a—open
2. bursa copulatrix	d—absent	d—absent	a/d—present or absent	a/d—present or absent
3. larva	d—echinospira	d—echinospira	a—veliger	a—veliger
4. osphradium	a—bipectinate	a—bipectinate	d—triradiate	d—triradiate
5. jaws	a—separate	d—united	a—separate	a—separate
6. lateral radular teeth	a—undivided	a—undivided	d—serrate	a—undivided

a—ancestral; d—derived

The status of *Pedicularia* has also been a controversial aspect of the systematics of the Lamellariacea and Cypraeacea. Schilder (1936) considered the Pedicularinae as a subfamily of the Ovulidae (as Amphiperatidae) but later (1966) considered them as a distinct family in the Triviacea. The internal morphology of *Pedicularia* is largely unknown, with the exception of the radula. Schilder's (1966: 31) transfer of *Pedicularia* from the Ovulidae to the Triviacea appears to be largely based on the fact that its placement was altered in *Zoological Record*. Subsequent authors have merely followed Schilder's placement of *Pedicularia* in the Triviacea.

The fact that *Pedicularia* possesses a trifid osphradium suggests that it is allied to the Cypraeacea. It has none of the derived features uniting the Lamellariacea, although the larval stage remains unknown. The accessory

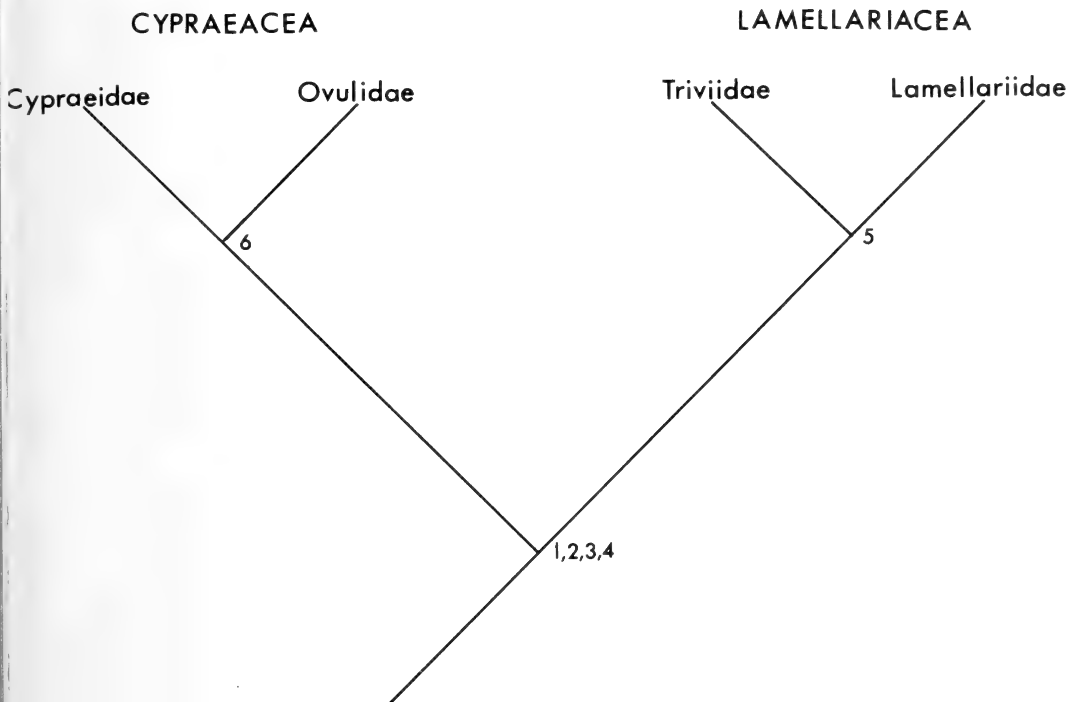

Fig. 35. Phylogeny of the Cypraeacea and Lamellariacea.
(Numbers refer to characters listed in Table 1.)

prostate described here for *Pedicularia* has not been previously observed in any other prosobranch. It may serve as a unique modification separating the Pediculariidae from the Ovulidae. However, no morphological information is available on other *Pedicularia* species and *Cyphoma* is the only ovulid for which details of the morphology are known (Ghiselin & Wilson 1966). Until the morphological variability of these taxa is more completely understood we prefer to retain *Pedicularia* in the Ovulidae.

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ABBREVIATIONS

a	ampulla	dd	digestive diverticulum
al	albumen gland	dg	digestive gland
an	anus	e	eye
bc	bursa copulatrix	eg	oesophageal gland
bm	buccal mass	f	foot
c	cerebral ganglion	h	heart
ct	ctenidium	hg	hypobranchial gland

i	intestine	pr	prostate
j	jaw	ra	radula
k	kidney	rs	receptaculum seminis
m	mantle	s	siphon
me	membrane gland	sb	subintestinal ganglion
mu	mucous gland	sg	sperm groove
od	oviduct	sp	supraintestinal ganglion
oe	oesophagus	st	stomach
os	osphradium	t	testis
ov	ovary	te	tentacle
p	penis	v	visceral ganglion
pe	pedal ganglion	♀ a	female aperture
pl	pleural ganglion		

NOTE

While this paper was in press Burgess (1985) was published, in which *Cypraea lisetae* Kilburn, 1975, was synonymized with *Pustularia maricola* Cate, 1976. The range of *C. lisetae* is thus extended to the Philippines and Solomon Islands, so that it can no longer be regarded as endemic to southern Africa.

References:

BURGESS, C. M. 1985. *Cowries of the world.* Cape Town: Seacomber Publications.
CATE, C. N. 1976. Three new cypraeacean species (Mollusca: Gastropoda). *Veliger* **18**: 383–384.

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers.

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .': '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
(c) Scientific names, but not their vernacular derivatives
e.g.Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

TERRENCE M. GOSLINER
&
WILLIAM R. LILTVED

ASPECTS OF THE MORPHOLOGY OF THE ENDEMIC SOUTH AFRICAN CYPRAEIDAE WITH A DISCUSSION OF THE EVOLUTION OF THE CYPRAEACEA AND LAMELLARIACEA

96 PART 5 DECEMBER 1985 ISSN 0303-2515

ANNALS OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

INSTRUCTIONS TO AUTHORS

1. MATERIAL should be original and not published elsewhere, in whole or in part.

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(a) *Centred masthead to consist of*
Title: informative but concise, without abbreviations and not including the names of new genera or species
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Number of illustrations (figures, enumerated maps and tables, in this order)
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Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including caption); the reduction or enlargement required should be indicated (and preferably uniform); originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the caption; if the latter, then the final reduction or enlargement should be taken into consideration.

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FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88** (3): 100–140.
FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.
THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

(continued inside back cover)

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TURONIAN, CONIACIAN, AND SANTONIAN OSTRACODA FROM SOUTH-EAST AFRICA

By

R. V. DINGLE

Cape Town Kaapstad

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TURONIAN, CONIACIAN, AND SANTONIAN OSTRACODA FROM SOUTH-EAST AFRICA

By

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Marine Geoscience Unit, Department of Geology, University of Cape Town

(With 53 figures and 18 tables)

[*MS accepted 18 January 1985*]

ABSTRACT

Fifty-five species, representing at least twenty genera, are recorded from the Turonian to Santonian strata of Zululand (Mfolozi Valley–False Bay area and Richards Bay borehole), offshore Natal (J(c)–1 borehole), Transkei (Umzamba), and Agulhas Bank. Three species are new: *Cytherelloidea mtubaensis, Cythereis mfoloziensis* and *Unicapella stragulata*. Palaeoecological analyses suggest that depositional environments at the three sites in Zululand all commenced with shallow-water conditions that progressively deepened, but there is evidence of local shallowing in the False Bay area in Upper Santonian times as a result of increased sediment supply. A faunal boundary is recognized between southern outcrops (Umzamba) and Zululand during the Santonian. This is speculated to have been temperature-controlled, and regional considerations of palaeogeography and biogeography suggest that the major ostracod faunal dichotomy across the Turonian–Coniacian boundary in south-east Africa was caused by the influx of warm-water faunas from tropical stocks in the Brazil–Gabon area of the Atlantic. This was initiated by the breakdown of the Walvis–Rio Grande barrier and establishment of a clockwise ocean-current circulation pattern in the southern South Atlantic, which injected warm water into existing north-east flowing currents off the coast of south-east Africa. By comparison with Tanzanian faunas, the timing of this is dated between Lower Cenomanian and Middle Turonian (i.e. between 99 and 89 m.y. ago), and probably coincided with the Lower Turonian transgression recognized in Nigeria (*c.* 91 m.y.).

An ostracod zonation scheme comprising four zones is proposed for the Coniacian–Santonian strata of south-east Africa.

CONTENTS

Ann. S. Afr. Mus. **96** (5), 1985: 123–239, 53 figs, 18 tables.

INTRODUCTION

In south-east Africa there is a widespread hiatus between sediments of mid-Cretaceous age, and overlying strata that were deposited during the Upper Cretaceous transgression (Kennedy & Klinger 1971). Ammonite studies by Kennedy & Klinger (1975) show that at outcrop in the Zululand–Natal region this non-sequence spans uppermost Cenomanian IV to lowermost Coniacian I time, although in north Zululand and offshore Natal, Upper Turonian strata have been proved in oil-exploration boreholes (Du Toit & Leith 1974; McLachlan & McMillan 1979). Preliminary studies showed that this important lithostratigraphic break coincides with a first-order biostratigraphic dichotomy in the ostracod faunas of south-east Africa, and that there is strong evidence for the event having regional significance (Dingle 1982). What makes these phenomena of particular interest is the probability that the faunal change can be related to plate-tectonic events in the South Atlantic, and specifically, the breaching of the Walvis Ridge–Rio Grande Rise archipelago as a faunal barrier between the Equatorial (Brazil–West Africa) and southern Atlantic–south-west Indian ocean provinces. The purpose of this contribution is twofold: to document the Turonian to Santonian

ostracods of south-east Africa; and to make regional faunal comparisons and discuss their palaeogeographical implications.

Known outcrops of Coniacian and Santonian sediments in south-east Africa are limited to the Zululand–Natal coastal plain, northern Transkei (Umzamba), and the western Agulhas Bank (Fig. 1), although borehole and geophysical evidence indicate that they occur extensively beneath younger cover on the continental shelves around southern Africa (Dingle *et al.* 1983). We have examined samples from all three areas, including material from borehole J(c)–1 offshore Natal, but only in Zululand are outcrops extensive and referable to all of the Coniacian and Santonian ammonite stages recognized by Kennedy & Klinger (1975). No Turonian outcrops have been reported from southern Africa, and samples of this age were available only from the J(c)–1 borehole. A summary of the spatial and temporal distribution of the ostracods recovered during this project is shown in Table 1.

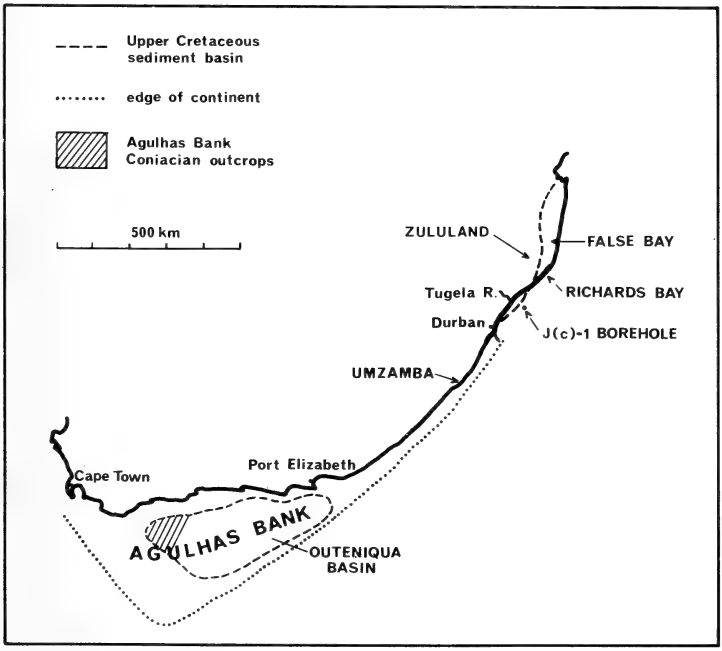


Fig. 1. Turonian to Santonian sample localities in south-east Africa.

TABLE 1

Temporal and spatial distribution of Turonian to Santonian ostracods in south-east Africa.

	Upper Turonian**	Coniacian I	II	III	IV	V	Santonian I	II	III		Zululand FB	MV	BH9	Um.	Ag. Bank
1 *Cytherella* sp. 1929					x							x			
2 *Cytherella* sp. 2351								x	x		x				
3 *Cytherella* sp. 1–4								x	x	*			x		
4 *Cytherelloidea mtubaensis*					x							x			
5 *Cytherelloidea newtoni*					x			x	x		x	x	x		
6 *Cytherelloidea umzambaensis*					x			x	x	*	x	x	x	x	
7 *Cytherelloidea gardeni*								x	x				x	x	
8 *Cytherelloidea griesbachi*									x	*			x	x	
9 *Apateloschizocythere?* cf. *mclachlani*			x												x
10 *Amphicytherura tumida*								x	x	*			x	x	
11 *Brachycythere agulhasensis*			x												x
12 *Brachycythere longicaudata*	x			x	x			x	x	*	x	x	x	x	
13 *Brachycythere rotunda*								x						x	
14 *Brachycythere pondolandensis*								x	x				x	x	
15 *Brachycythere sicarius*								x	x	*	x	x	x	x	
16 *Cythereis klingeri*					x			x	x	*	x	x	x		
17 *Cythereis luzangaziensis*	x				cf. x							x			
18 *Cythereis mfoloziensis*				x								x			
19 *Cythereis transkeiensis*								x	x	*		x	x	x	
20 *Gibberleberis africanus*					x			x	x		x	x	x	x	
21 *Gibberleberis elongata*									x	*			x		
22 *Rayneria nealei*					x			x	x	*		x	x	x	
23 *Haughtonileberis haughtoni*	x				x			x	x	*	x	x	x	x	
24 *Haughtonileberis fissilis*								x	x	*		x	x	x	
25 *Haughtonileberis vanhoepeni*									x	*			x		

30 *Bythocypris richardsbayensis*		x	x	x	*	x	x	x		
31 *Paraphysocythere thompsoni*			x	x					x	
32 *Veenia obesa*			x	x					x	
33 *Bairdoppilata andersoni*			x	x	*	x	x	x	x	
34 *Cnestocythere?* sp. 2091				x					x	
35 *Pondoina sulcata*			x	x				x	x	
36 *Unicapella stragulata*		x	x	x		x	x			
37 Indet. sp. 1874			x			x				
38 Indet. sp. 1956		x					x			
39 Indet. sp. 2103			x						x	
40 Indet. sp. 2104			x						x	
41 Indet. sp. 2108			x						x	
42 Indet. sp. 2078				x					x	
43 Indet. sp. 2125			x			x				
44 Indet, sp. 1232		x					x			

J(c)–1	Cen.–Tur.	Coniacian	Santonian	
45 *Bairdoppilata* sp. 2327	x			
46 *Bairdoppilata* sp. 2322			x	
47 *Bairdoppilata* sp. 2336	x		x	
48 *Bythocypris richardsbayensis*	x		x	
49 *Cytherella* sp. 2325		x		
50 *Cytherella* sp. 2317			x	
51 *Krithe* sp. 2329	x			
52 *Krithe* sp. 2332	x			
53 *Dutoitella mimica*			x	*
54 Indet. sp. 2312	x			
55 Indet. sp. 2314	x			

** = Tanzania, * = extension above Santonian III; FB = False Bay, MV = Mfolozi Valley, BH9 = Richards Bay borehole; Um = Umzamba, Ag. Bank = Agulhas Bank.

TABLE 1

Temporal and spatial distribution of Turonian to Santonian ostracods in south-east Africa.

	Upper Turonian**	Coniacian I	Coniacian II	Coniacian III	Coniacian IV	Coniacian V	Santonian I	Santonian II	Santonian III		Zululand FB	Zululand MV	Zululand BH9	Um.	Ag. Bank
1 *Cytherella* sp. 1929					x							x			
2 *Cytherella* sp. 2351								x	x		x				
3 *Cytherella* sp. 1–4								x	x	*			x		
4 *Cytherelloidea mtubaensis*					x							x			
5 *Cytherelloidea newtoni*					x	—	—	x	x		x	x	x		
6 *Cytherelloidea umzambaensis*					x	—	—	x	x	*	x	x	x	x	
7 *Cytherelloidea gardeni*								x	x				x	x	
8 *Cytherelloidea griesbachi*									x	*			x	x	
9 *Apateloschizocythere?* cf. *mclachlani*			x												x
10 *Amphicytherura tumida*								x	x	*			x	x	
11 *Brachycythere agulhasensis*			x												x
12 *Brachycythere longicaudata*	x	—	—	x	x	—	—	x	x	*	x	x	x	x	
13 *Brachycythere rotunda*								x						x	
14 *Brachycythere pondolandensis*								x	x				x	x	
15 *Brachycythere sicarius*								x	x	*	x	x	x	x	
16 *Cythereis klingeri*					x	—	—	x	x	*	x	x	x		
17 *Cythereis luzangaziensis*	x	—	—	—	cf. x							x			
18 *Cythereis mfoloziensis*				x								x			
19 *Cythereis transkeiensis*								x	x	*		x	x	x	
20 *Gibberleberis africanus*					x	—	—	x	x		x	x	x	x	
21 *Gibberleberis elongata*									x	*			x		
22 *Rayneria nealei*					x	—	—	x	x	*		x	x	x	
23 *Haughtonileberis haughtoni*	x	—	—	—	x	—	—	x	x	*	x	x	x	x	
24 *Haughtonileberis fissilis*								x	x	*		x	x	x	
25 *Haughtonileberis vanhoepeni*									x	*			x		
26 *Oertliella pennata*					x	—	—	x	x	*	x	x	x	x	
27 *Oertliella* sp. 476								x	x	*			x		
28 *Paracypris umzambaensis*								x	x	*	x	x	x	x	
29 *Paracypris zululandensis*					x	—	—	x	x	*	x	x	x		
30 *Bythocypris richardsbayensis*					x	—	—	x	x	*	x	x	x		
31 *Paraphysocythere thompsoni*								x	x					x	
32 *Veenia obesa*								x	x					x	
33 *Bairdoppilata andersoni*								x	x	*	x	x	x	x	
34 *Cnestocythere?* sp. 2091									x					x	
35 *Pondoina sulcata*								x	x				x	x	
36 *Unicapella stragulata*					x	—	—	x	x		x	x			
37 Indet. sp. 1874								x			x				
38 Indet. sp. 1956					x							x			
39 Indet. sp. 2103								x						x	
40 Indet. sp. 2104								x						x	
41 Indet. sp. 2108								x						x	
42 Indet. sp. 2078									x					x	
43 Indet. sp. 2125								x			x				
44 Indet, sp. 1232					x							x			

J(c)–1	Cen.–Tur.	Coniacian	Santonian	
45 *Bairdoppilata* sp. 2327	x			
46 *Bairdoppilata* sp. 2322			x	
47 *Bairdoppilata* sp. 2336	x	—	x	
48 *Bythocypris richardsbayensis*	x	—	x	
49 *Cytherella* sp. 2325		x		
50 *Cytherella* sp. 2317			x	
51 *Krithe* sp. 2329	x			
52 *Krithe* sp. 2332	x			
53 *Dutoitella mimica*			x	*
54 Indet. sp. 2312	x			
55 Indet. sp. 2314	x			

** = Tanzania, * = extension above Santonian III; FB = False Bay, MV = Mfolozi Valley, BH9 = Richards Bay borehole; Um = Umzamba, Ag. Bank = Agulhas Bank.

SAMPLING LOCALITIES

Zululand and Richards Bay

Coniacian and Santonian sediments crop out in river valleys in a north–south swathe along the central part of the Zululand coastal plain between Kwa-Mbonambi in the south (where they are overstepped by Campanian strata), and the Mkuze River in the north. Farther north, along the Pongola River and under the Makatini Flats, no outcrops have been recorded, but they probably underlie Neogene sands. South of Hluhluwe River, Coniacian oversteps the Albian–Cenomanian Mzinene Formation to rest directly on volcanic basement. Kennedy & Klinger (1975) have collected extensively from these exposures, and we have retained their locality and bed-number notation. (Quotation is in the form: locality–bed number/subdivision.) Biostratigraphic subdivision of the two stages follows that of Kennedy & Klinger (1975), and to facilitate international correlation of the ostracod time ranges we quote their ammonite zonation characteristics in Table 2.

South of the Mfolozi valley there are no good natural outcrops, but samples have been obtained from the Richards Bay borehole (BH9), which spans the Santonian–Campanian boundary. At this locality Santonian II rests directly on basement. A similar succession was recorded by Kennedy & Klinger (1975) in an excavation on the Nyokanemi River at Kwa-Mbonambi. These records indicate that Coniacian–Santonian I is missing over a basement feature that Dingle *et al.* (1983) refer to as the Richards Bay Arch. Farther south (Durban), Santonian II is missing, and only Santonian III or Campanian strata are present (Fig. 3).

In Zululand, the Coniacian and Santonian form the lower part of the St. Lucia Formation. It has a basal conglomerate with igneous pebbles, agates, bivalve debris and abundant *Pterotrigonia shepstoni*, but overall consists predominantly of silts with concretionary siltstones and shelly limestones (Kennedy & Klinger 1975; Dingle *et al.* 1983).

Although all the ammonite zones were sampled for ostracods, many of the samples were barren, presumably because of decalcification. The oldest zone that contained ostracods was Coniacian III at locality 16 (28°26,70′S 32°11,42′E), a small quarry on the north side of the Mfolozi River, south of Mtubatuba. Coniacian IV was sampled at locality 15 (28°26,58′S 32°11,40′E) in another small quarry 175 m west of locality 16, and 45 km north-north-east at locality 89 (28°02,27′S 32°21,32′E). The latter consists of hill slopes north of the Hluhluwe River where it debouches into False Bay. No Lower Santonian ostracod-bearing samples were available, but good faunus occurred in samples from outcrops covering the upper part of Santonian II and most of Santonian III. The former are exposed in cliff sections along the western shore of False Bay at locality 74 (27°54,20′S 32°23,78′E). Santonian III faunas were also obtained from locality 74, where the higher beds in the cliff dip to the north-east and crop out along the shore, and at locality 14 (28°28,40′S 32°10,72′E). The latter is near the road

TABLE 2

Kennedy & Klinger's (1975) ammonite zonation of Coniacian to Santonian strata in Zululand.

SANTONIAN

Santonian III

Hauericeras gardeni is abundant. The remainder of the fauna is relatively scarce and is made up of: *Plesiotexanites stangeri* and varieties, *Texanites soutoni, Texanites* spp., *Pseudoschloenbachia, ?Eupachydiscus, Hyphantoceras, Reginaites, Submortoniceras, Bevahites* and diplomoceratids.

Santonian II

Plesiotexanites stangeri and varieties are abundant. The remainder of the fauna consists of: *Texanites soutoni, Texanites* spp., *Hauericeras, Pseudoschloenbachia, ?Eupachydiscus, Hyphantoceras* and diplomoceratids.

Santonian I

Texanites oliveti, Plesiotexanites stangeri, P. densicosta and *P. sparsicosta, Eutexanites, Paratexanites, Hauericeras gardeni, Pseudoschloenbachia, Pseudophyllites indra, ?Karapadites, ?Eupachydiscus, Gaudryceras, Hyphantoceras* and diplomoceratids.

The local base is drawn at the level of the appearance of *Texanites* s.s. in numbers.

CONIACIAN

Coniacian V

Abundant baculitids ornamented only by growth striae. Also forms resembling *Pseudoschloenbachia primitiva* Collignon. *Scaphites, Tetragonites, Protexanites, Texanites* and *Paratexanites* occur.

Coniacian IV

Baculites gr. *capensis* are abundant, and compressed, finely ornamented peroniceratids, *Zuluites* and robustly ornamented *?Gauthiericeras* (e.g. *'Falsebayites', 'Fluminites', 'Hluhluweoceras'* and *'Andersonites'* of Van Hoepen) are locally common. *Tetragonites, Protexanites* and *Paratexanites* also occur.

Coniacian III

Placenticeras, coarsely ornamented peroniceratids *(Zuluiceras), Protexanites, Miotexanites, Paratexanites bailyi, Kossmaticeras* and *?Praemuniericeras* are common.

Coniacian II

Proplacenticeras kaffrarium is abundant. *Peroniceras* gr. *tridorsatum* and *Forresteria* are common. Other types include: *'Eedenoceras' multicostatum, Basseoceras krameri, Kossmaticeras sparsicosta, K. sakondryense, Puzosia* spp., *Pachydesmoceras, Lewesiceras australe, Yabeiceras* spp., *Pseudoxybeloceras matsumotoi, Hyphantoceras reussianum, Allocrioceras* spp., *Baculites bailyi, Scaphites meslei* and *Protexanites.*

Coniacian I

Proplacenticeras kaffrarium is abundant. Other types include *Kossmaticeras theobaldianum, Bostrychoceras indicum, Pachydesmoceras denisonianum* and *Pachydesmoceras* sp.

The local base is drawn at the level of appearance of *Kossmaticeras theobaldianum.*

TURONIAN

No Turonian rocks known from outcrop in Zululand. They occur at depth in boreholes in northern Zululand.

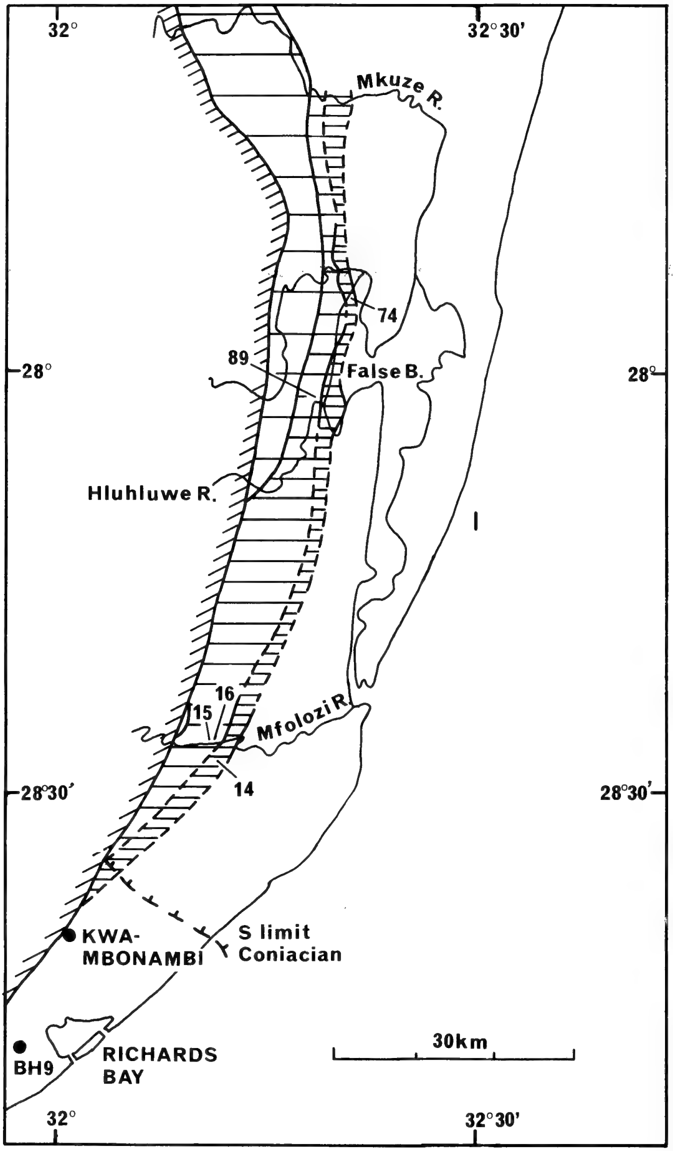


Fig. 2. Sampling localities in Zululand, using the notation of Kennedy & Klinger (1975). See text for co-ordinates and outcrop details. Geology is after Kennedy & Klinger (1975) and Dingle *et al.* (1983) and the key is in Figure 3. BH9 is the Richards Bay borehole.

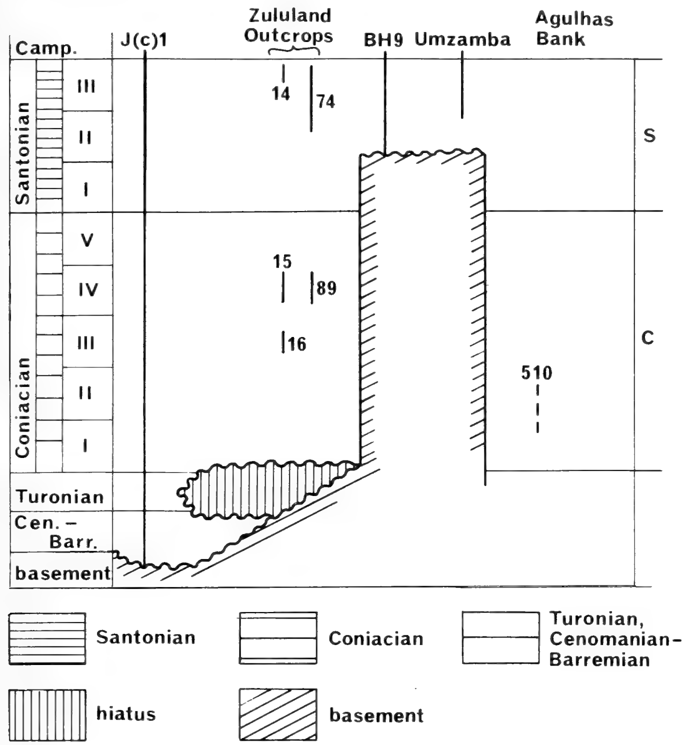


Fig. 3. Correlation chart for sampled sections (see Figs 1 and 2 for locations). Roman numerals indicate ammonite zones after Kennedy & Klinger (1975) (see Table 2 for details). There is some uncertainty as to the ammonite zones represented in the Agulhas Bank outcrops.

bridge over the Msunduzi River due south of River View in the Mfolozi River valley near Mtubatuba.

The Richards Bay borehole BH9 is located at the southern end of the Zululand coastal plain, and 23 cored sections were available for study, covering the whole sequence from immediately above bedrock (Santonian II) to the Santonian–Campanian boundary. The borehole succession and details of sampled horizons are given in Klinger & Kennedy (1977) and Dingle (1980). Ostracods from BH9 have previously been described by Dingle (1980), and serve as an important link between the north Zululand assemblages and the southern assemblages from Umzamba.

Umzamba

The most recent biostratigraphic zonations of this classic locality have been by Klinger & Kennedy (1977, 1980) using ammonites, and Makrides (1979) using foraminifera. Klinger & Kennedy (1980) date the lowermost ammonite-bearing

beds in the Umzamba area (locality C bed 3) as Santonian II (Fig. 4), and place the Santonian II–III boundary within bed 3 at locality A.The latter is the cliff section immediately north of the Umzamba River mouth, from which Dingle (1969) described the ostracods from four horizons, and from which additional material was collected for the present study (31°05,83′S 30°10,50′E). For a comprehensive summary of the stratigraphy and correlation of the Umzamba

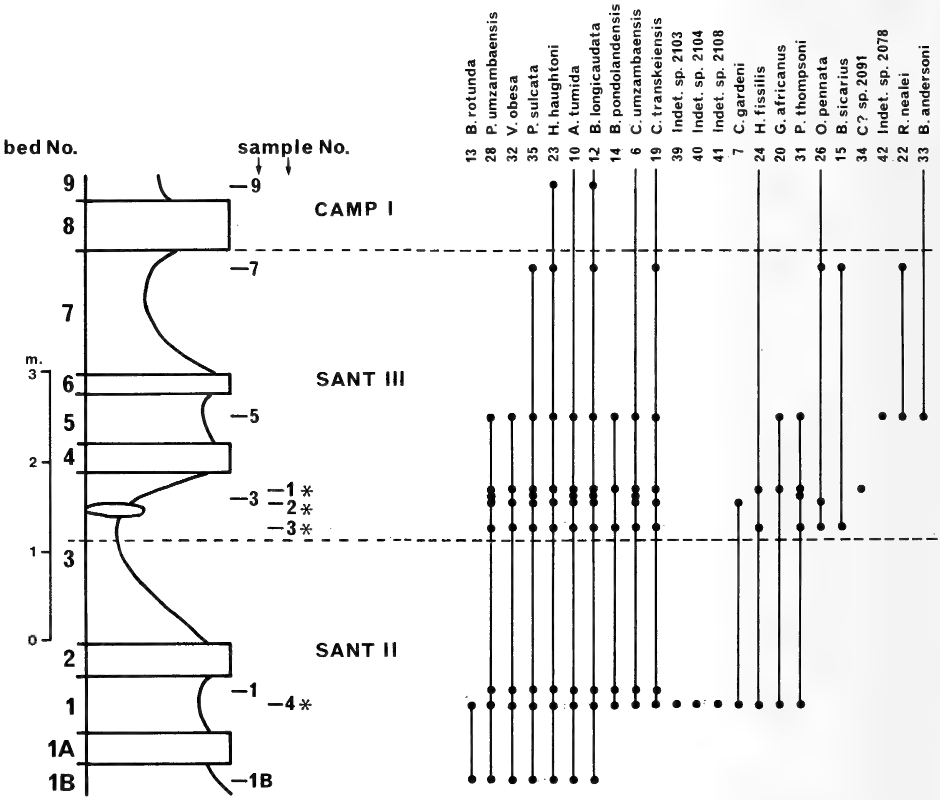


Fig. 4. Measured section at Umzamba Cliff using the bed numbers of Klinger & Kennedy (1980). Ostracod distributions relate to this notation, in addition to that presented by Dingle (1969) (right-hand column, with stars, under 'sample No.'). Ostracod numbers refer to informal taxa numbers on Table 1.

Formation in adjacent outcrops the reader is referred to Dingle *et al.* (1983). It is important to note that at both Umzamba and Richards Bay, Santonian II, which is locally the oldest representative of the Upper Cretaceous transgression, consists of shallow-water sediments deposited in relatively high-energy environments. In contrast, sediments of the same age in north Zululand were probably deposited under relatively deep-water conditions (see Discussion).

Outeniqua Basin (Agulhas Bank)

Three Lower Coniacian samples have been dredged from the western Agulhas Bank during University of Cape Town geological surveys of the sea floor (Fig. 1), and Klinger *et al.* (1976, 1980) have described their ammonite and bivalve faunas (Table 3). One sample (TBD 510) contained ostracods, which were described by Dingle (1971*b*), who quoted a date of Lower–Middle Senonian, based on the presence of the planktonic foraminifera *Globotruncana* sp. ex gr. *G. marginata*, identified by Dr H. P. Luterbacher (University of Tübingen). The ostracods are re-illustrated and their taxonomy is revised.

TABLE 3

Ammonites and bivalves in Lower Coniacian samples from the Agulhas Bank (data from Klinger *et al.* 1976, 1980).

TBD 510: 35°11,70′S 20°30,00′E
Proplacenticeras kaffrarium (Etheridge, 1904)
Scaphites (Otoscaphites?) sp.
TBD 4492: 35°10,00′S 20°53,00′E
Yabeiceras manasoaense Collignon, 1965
TBD 4510: 35°2,50′S 20°39,50′E
Inoceramus (I.) ernsti Heinz, 1928
I. frechi Flegel, 1905

J(c)–1 borehole, offshore Natal

Twenty-five sediment samples (of which 12 contained ostracods) were available from the lower part of the J(c)–1 borehole on the continental shelf off Natal at 29°27,69′S 31°35,66′E in 72 m of water. The borehole penetrated about 2 000 m of Tertiary and Cretaceous strata on the upper part of the Tugela Cone before entering Palaeozoic quartzites, and the section between 2 297 m and 1 927 m (370 m) is considered Upper Cenomanian to Santonian in age (Table 4). The Turonian section (2 197–2 127 m, 70 m) in this borehole is the only one of its age from which material is available in southern Africa. Ostracod faunas from the Campanian to Oligocene sections have previously been described by Dingle (1976, 1981).

PREVIOUS WORK

Chapman's (1904) pioneer work on South African ostracod faunas was undertaken on Santonian material from Umzamba, and was followed by a further publication on a fauna from the same strata in 1923. Unfortunately, all the type material relating to these two studies was destroyed in 1953 (see Dingle 1969 for details). This fact, combined with poor illustrations and ambiguous descriptions in the publications, as well as lack of precise locality details, makes comparative studies with the taxa he identified extremely difficult, and in most cases impossible. Dingle (1969) redescribed the faunas from Santonian II and III strata at the main Umzamba cliff section (Klinger & Kennedy's (1980) locality A), and

TABLE 4

Upper Cenomanian to Santonian ostracods from the J(c) – 1 borehole.

Age*	Depth**		Ostracods															
			Bairdoppilata sp.				*Dutoitella*	*Bythocypris* cf.	*Cytherella* sp.		*Krithe* sp.		Indet.					
	m	ft	2336	2322	2327	Frag.	*mimica*	*richardsbayensis*	2317	2325	2332	2329	sp.	2314	2312	Pyr.	*Ino.*	Charo.
Sant.	1 945	6 380															x	
	1 981	6 500	x	x														x
	2 006	6 580															x	
	2 018	6 620														x	x	
	2 030	6 660					x	x										x
	2 042	6 700							x							x	x	
	2 054	6 740														x	x	
	2 067	6 780														x	x	
	2 079	6 820														x	x	
	2 103	6 900														x	x	
Con.	2 115	6 940								x							x	
	2 128	6 980																
	2 140	7 020											x					
	2 152	7 060			x							x						
Tur.	2 176	7 140									x		x					x
	2 188	7 180																
	2 201	7 220										x						
	2 213	7 260	x					x						x	x			
U. Cen.	2 225	7 300				x							x					
	2 237	7 340				x												
	2 249	7 380																
	2 262	7 420																
	2 274	7 460																
	2 286	7 500											x					
	2 297	7 540																
Palaeozoic basement																		

* = stratigraphy after Du Toit & Leith (1974), McLachlan & McMillan (1979), and Dingle *et al.* (1983).
** = original depths in feet shown for correlation with earlier works.
Frag. = fragment, Pyr. = pyrite, *Ino.* = *Inoceramus* prisms, Charo. = charophytes. Indet. sp. refers to various indeterminate fragments

during the course of the present study two additional Santonian II and three Santonian III ostracod-bearing samples were collected. In particular, the upper part of the Santonian III was sampled. The only other descriptions of Santonian ostracods were by Dingle (1980) on the Santonian II and III faunas from the Richards Bay borehole (BH9). There have been no previous published studies on South African Coniacian ostracods, nor on Santonian material from the outcrops in north Zululand.

No Turonian strata are known to crop out in south-east Africa, but details of ostracod populations of this age from Tanzania (Bate & Bayliss 1969) (Table 5), Gabon (Grosdidier 1979), and Brazil and Gabon (Krömmelbein 1964, 1972) form important sources of information for understanding the development of post-mid-Cretaceous ostracod faunas in south-east Africa. Three ostracod-bearing samples of Turonian age were available from the J(c)–1 borehole for the present study.

TABLE 5

Taxa recorded by Bate (*in* Bate & Bayliss 1969) from Tanzania.

A. Sample BM75, Upper Turonian (Luzangazi Stream, north of Wami River).

Ostracoda	Planktonic foraminifera
Cytherura moorei	*Globotruncana helvetica* Bolli
Cytherura luzangaziensis	*Globotruncana linneiana* (d'Orbigny)
Isocythereis sp., Io782	*Globotruncana linneiana coronata* (Bolli)
Curfsina turonica†	*Globotruncana* spp.
Akrogmocythere wamiensis	*Clavihedbergella* sp.
Brachycythere aff. *sapucariensis**†	*Hedbergella delrioensis* (Carsey)
Cythereis luzangaziensis†	*Hedbergella* sp.
Cythereis sp. C, Io793	*Heterohelix* sp.
Paracypris wamiensis	*Praeglobotruncana* sp.
Sphaeroleberis africana	
Cytherella afroturonica	
Cytherelloidea turonica	

* = dominant taxon † = illustrated herein

B. Albian–Cenomanian

Albian	Cenomanian
Ovocytheridea mackinlayi	*Cythereis lindiensis*
Cytherelloidea sp. A	*Cytherella nalukundiensis*
Cythereis sp. A	*Cythereis* sp. B
Cytheropteron africanum	*Cytherelloidea cenomanica*
Cytherella postcontracta	*Majungaella pyriformis*
Majungaella pyriformis	*Cythereis africanus*
Cythereis africanus	
Genus A	
Macrocypris acuticaudata	

A total of 66 fossiliferous samples were available for study (53 from onshore, 12 from the J(c)–1 borehole, and one from the Agulhas Bank), from which 55 species of ostracods have been identified. Microfossils were extracted by washing and sieving, and were photographed with Cambridge S180 and S200 SEMs at the University of Cape Town. Specimens were mounted on double-sided Sellotape or water-soluble glue, and were coated with a gold–palladium mixture. Types and illustrated material are deposited in the South African Museum, Cape Town.

LIST OF GENERA

The genera of Ostracoda discussed in this work are given below:

SYSTEMATIC DESCRIPTIONS

The classification used here is based mostly on the Ostracod *Treatise* (Moore 1961), with various additions necessitated by recent work. Numeric taxonomic categories refer to unique SEM photographic negative numbers in the author's collection.

Abbreviations: ACA = anterior cardinal area; AM = anterior margin; ATE = anterior terminal element; CA = cardinal area; DM = dorsal margin; LV = left valve; MA = marginal area; ME = median element; MPC = marginal pore canal; MS = muscle scars; NPC = normal pore canal; PCA = posterior cardinal area; PM = posterior margin; PTE = posterior terminal element; RV = right valve; SCT = subcentral tubercle; VM = ventral margin.

Subclass OSTRACODA Latreille, 1806

Order PODOCOPIDA Müller, 1894

Suborder PLATYCOPINA Sars, 1866

Family **Cytherellidae** Sars, 1866

Genus *Cytherella* Jones, 1849

Cytherella sp. 1929

Fig. 5A

Remarks

This elongate species with prominent NPC is closest to *Cytherella* morphotype 3 that Dingle (1980) recorded from the Richards Bay borehole. There is a slight difference in their respective AM outlines, but the two may be conspecific.

Age and distribution

Coniacian IV, St. Lucia Formation, locality 15–1 to 15–5, Mtubatuba.

Cytherella sp. 2351

Fig. 5B

Remarks

An inflated species close to *Cytherella* morphotype 4 recorded by Dingle (1980) from the Santonian–Campanian II of the Richards Bay borehole.

Age and distribution

This species occurs consistently, though in small numbers, throughout the Santonian II–III section at locality 74, False Bay.

Cytherella sp. 2325

Fig. 5C

Remarks

A single broken carapace that has a vertically expanded, laterally compressed anterior area, an arched DM, and a convex VM.

Age and distribution

Coniacian, J(c)–1 borehole, 2 115 m (6 940 ft).

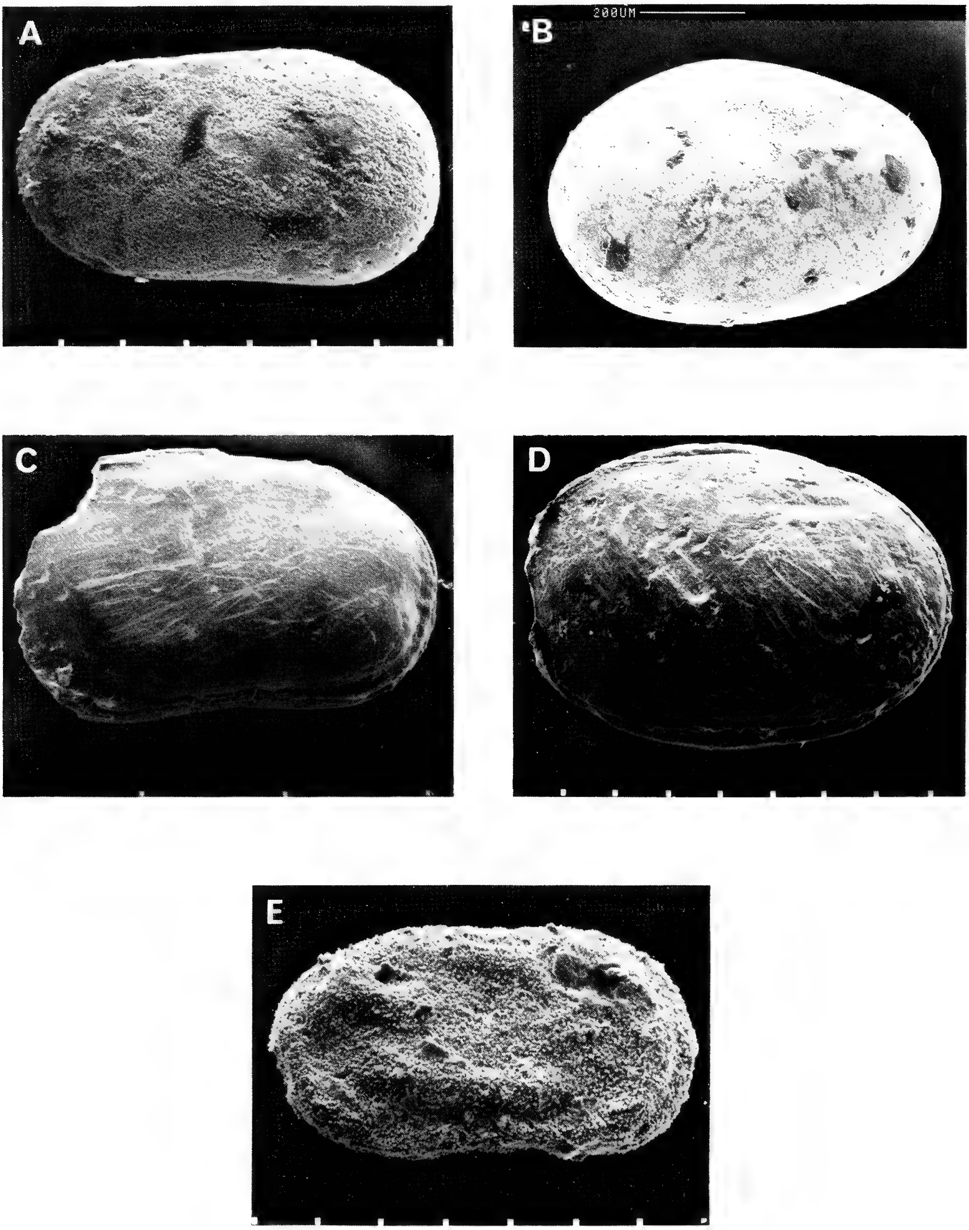


Fig. 5. A. *Cytherella* sp. 1929, SAM–PC6485, LV, locality 15–5, Mtubatuba, Coniacian IV. B. *Cytherella* sp. 2351, SAM–PC6486, RV, locality 74–9, False Bay, Santonian III. C. *Cytherella* sp. 2325, SAM–PC6487, LV, J(c)–1 borehole, 2 115 m, Coniacian. D. *Cytherella* sp. 2317, SAM–PC6488, LV, J(c)–1 borehole, 2 042 m, Santonian. E. *Cytherelloidea mtubaensis* sp. nov., SAM–PC6489, holotype, RV, locality 15–1, Mtubatuba, Coniacian IV, SEM 1954. Scale bars: A, D–E = 100 μ, B = 200 μ, C = 300 μ.

Cytherella sp. 2317

Fig. 5D

Remarks

A single carapace of an ovate species that is similar in outline to *Cytherella* morphotype 2 recorded by Dingle (1980) from the Santonian–Campanian II of the Richards Bay borehole.

Age and distribution

Santonian, J(c)–1 borehole, 2 042 m (6 700 ft).

Cytherella sp. 1–4 Dingle, 1980

Cytherella spp. 1, 2, 3, & 4. Dingle, 1980: 5–7, fig. 2A–F.
Cytherella sp. Dingle, 1981: 15–17, fig. 5A–F.

Remarks

Dingle (1980) recognized four morphotypes of *Cytherella* that he originally placed in separate categories, but subsequently gathered into one taxonomic unit because it was not possible to consistently discriminate the various valve outlines (Dingle 1981). See Dingle (1980) for representative illustrations.

Age and distribution

Examples of the four morphotypes occur sporadically throughout the Santonian II–III section of the Richards Bay borehole, but only appear in significant numbers in the Campanian. They range upwards into the Maastrichtian III, and two specimens of *Cytherella* (spp. 1929 and 2351) recorded from the Coniacian and Santonian II–III of Zululand outcrops during the present study may be conspecific. Better-quality material and larger populations need to be studied before further progress can be made in resolving the taxonomy of the Upper Cretaceous *Cytherella* species in Zululand.

Genus *Cytherelloidea* Alexander, 1929

This genus is the only one that is well represented above and below the mid-Cretaceous (Turonian–Coniacian) non-sequence in southern Africa, although none of its species range across the hiatus: seven species Berriasian to Cenomanian; seven species Coniacian to Maastrichtian. Of the seven post-Cenomanian species, three appear in the Coniacian (*C. mtubaensis, C. newtoni*, and *C. umzambaensis*); two in the Santonian (*C. gardeni* and *C. griesbachi*); and two in the Campanian (*C. contorta* and *C. mfoloziensis*) (Fig. 6).Three species (*C. mtubaensis, C. newtoni*, and *C. gardeni*) are restricted to Coniacian–Santonian strata, and only one has a relatively long range (*C. umzambaensis*—Coniacian IV to Campanian IV). *Cytherelloidea* is, therefore, a potentially useful genus for biostratigraphic work in the south-east African Coniacian to Maastrichtian sediments.

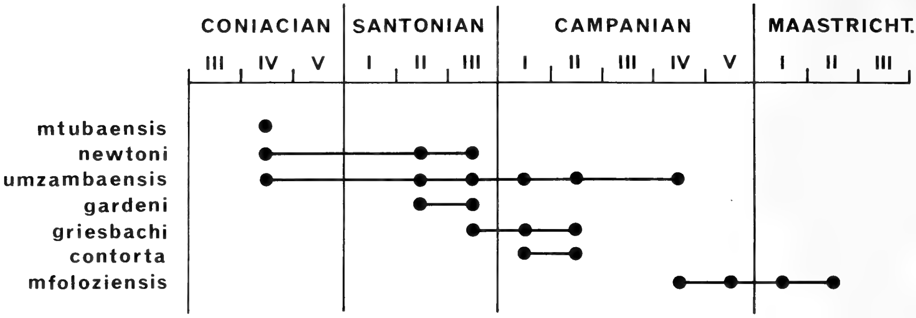


Fig. 6. Ranges of *Cytherelloidea* species in Upper Cretaceous strata of south-east Africa.

Cytherelloidea mtubaensis sp. nov.
Fig. 5E, 7A

Derivation of name

The name *mtubaensis* is derived from the type locality name Mtubatuba, Zululand.

Holotype

SAM–PC6489, RV, locality 15–1, Mtubatuba, Coniacian IV.

Diagnosis

Species with a continuous anterior, ventral, and posteroventral ridge; short elliptical ventromedian and dorsomedian to posterodorsal elevations.

Descriptions

External features. Broadly rounded AM and PM, straight to slightly convex DM, and a weakly concave VM. Surface elevations consist of a continuous, but relatively weak ridge that runs from the anterodorsal area via the VM to about mid-height on the PM. There is a prominent, short pseudo-elliptical ventromedian elevation and an irregular, continuous series of elevations and ridges in the dorsomedian to posterodorsal region. The most prominent part of the latter is at its posterior end. Surface otherwise apparently smooth.

No internal views seen.

Remarks

Only *C. griesbachi* Dingle, 1980 (Santonian III to Campanian III) has a surface rib pattern that is likely to be confused with that of *C. mtubaensis* (Fig. 7), because both have prominent short ventromedian elevations. However, the former has no ribs or elevations that run parallel to the PM, and has a ridge that is continuous around the DM and AM.

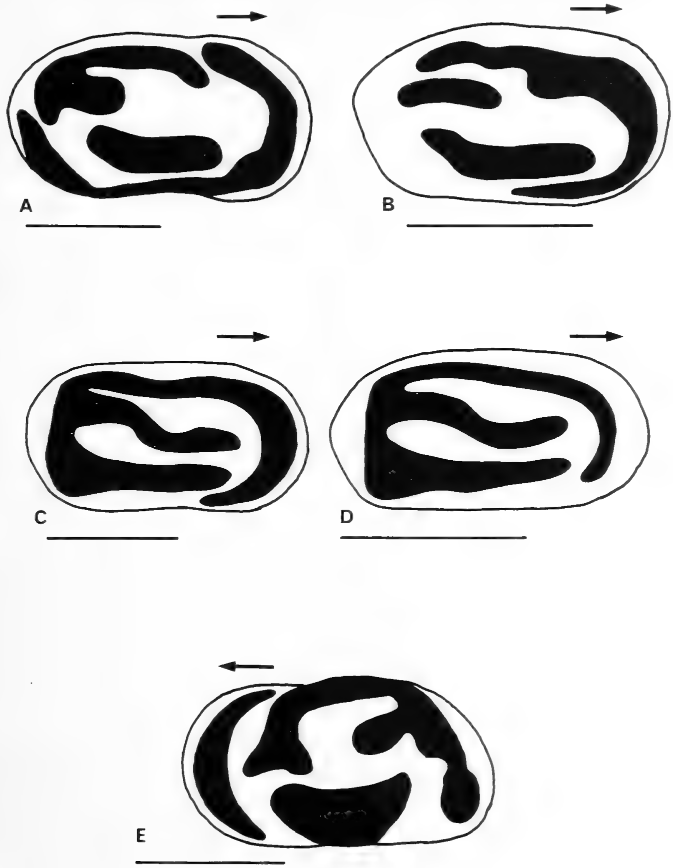


Fig. 7. Sketches of *Cytherelloidea* species, with positive features shaded. A. *C. mtubaensis* sp. nov., SAM–PC6489, holotype, RV, locality 15–1, Mtubatuba, Coniacian IV. B. *C. griesbachi*, holotype, SAM–K5575, RV, BH9 Richards Bay, 88,39 m, Campanian II. C. *C. umzambaensis*, SAM–PC6492, RV, locality 15–7, Mtubatuba, Coniacian IV, SEM 1953. D. *C. umzambaensis*, SAM–PC6491, RV, Umzamba bed 1, Santonian II, SEM 710. E. *C. newtoni*, SAM–PC6490, LV, locality 15–5, Mtubatuba, Coniacian IV, SEM 1919. Scale bars = 300 μ.

Dimensions (mm)

	length	height
PC6489	0,68	0,36

Age and distribution

Cytherelloidea mtubaensis is known only from the Coniacian IV at locality 15–1 at Mtubatuba, Zululand.

Cytherelloidea newtoni Dingle, 1980

Figs 7E, 8A–B

Cytherelloidea newtoni Dingle, 1980: 8–10, figs 3C, 4C.

Remarks

Small numbers of this distinctive species have been recorded from outcrops at Mtubatuba and False Bay, which show no significant morphological differences from the type material of the Richards Bay borehole.

Age and distribution

Cytherelloidea newtoni ranges Coniacian IV (Mtubatuba) to Santonian III (BH9 and False Bay). In the Richards Bay borehole it occurred in sediments deposited in environments that are thought to have ranged from shallow water, high energy, restricted circulation, through shallow water (<100 m), low energy, restricted circulation, to shallow, low-energy, open water (<100 m) (Dingle 1980). *Cytherelloidea newtoni,* although relatively rare, is probably a good stratigraphic indicator for Zululand Coniacian to Santonian strata.

Cytherelloidea umzambaensis Dingle, 1969

Figs 7C–D, 8C–D

Cytherella williamsoniana (*non* Jones, 1849) Chapman, 1904: 236.
Cytherelloidea umzambaensis Dingle, 1969: 351–353, fig. 3; 1980: 7, figs 3A, 4A–B; 1981: 18, figs 7A, 9C.

Remarks

This species is one of the distinctive elements of the Upper Cretaceous ostracod faunas of south-east Africa, and displays a high degree of morphological stability throughout its range. The median longitudinal ridge does show some variability in elevation along the section anterior of the MS depression.

Age and distribution

Cytherelloidea umzambaensis ranges Coniacian IV (Mtubatuba) to Campanian IV (Nibela Peninsula) at outcrop in Zululand, Santonian II to Campanian II in BH9, and Santonian II to Campanian I at Umzamba (type locality). Its distribution in the Richards Bay borehole suggests that it preferred quiet, moderate-depth (100–300 m) environments, but was tolerant of both shallow (<100 m), high-energy and deep (>500 m), low-energy situations.

Cytherelloidea gardeni Dingle, 1971

Fig. 8E–F

non *Cytherelloidea delicata* Dingle, 1969: 353–354, fig. 4.
Cytherelloidea gardeni Dingle, 1971*a*: 353.
Cytherelloidea cf. *C. gardeni* Dingle, 1980: 7.

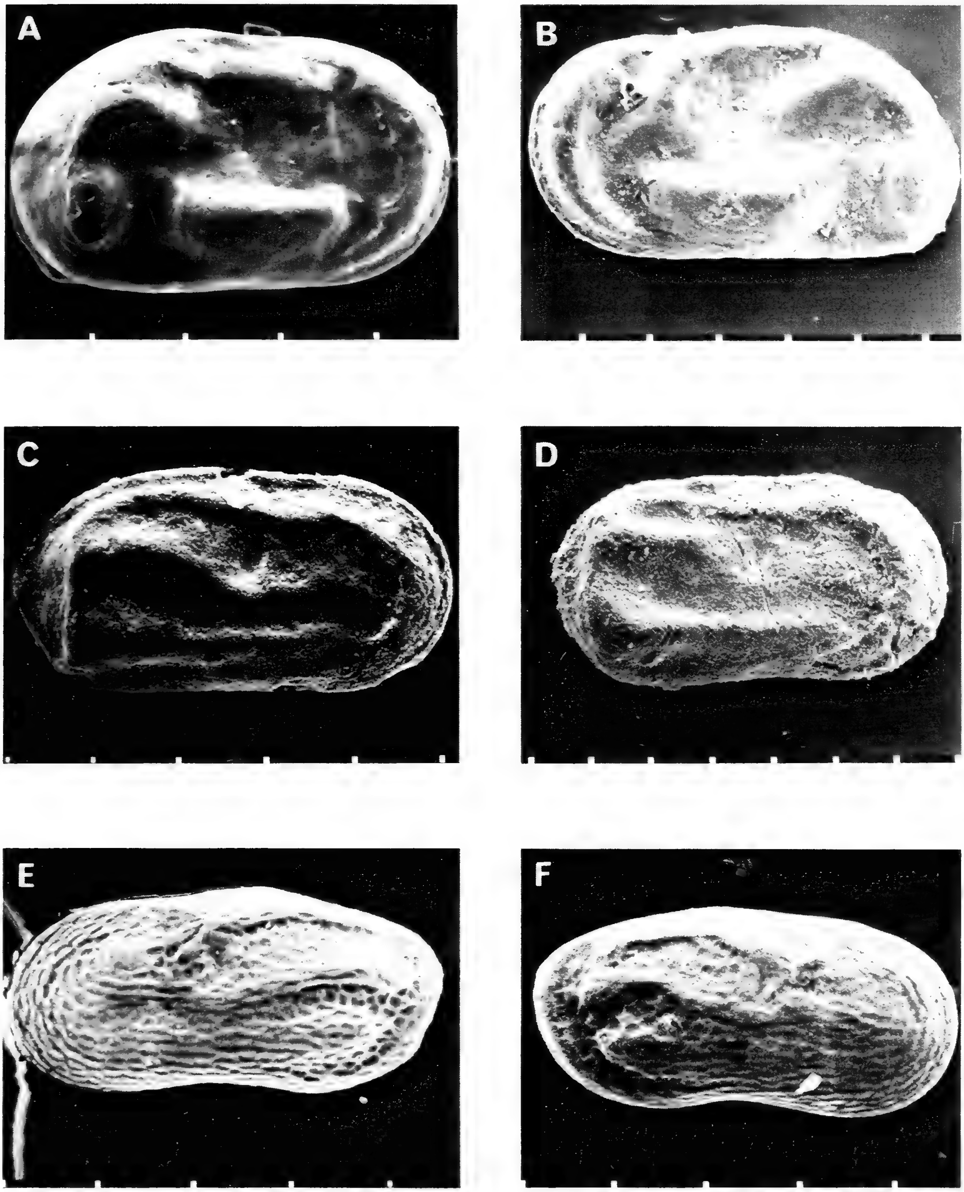


Fig. 8. Genus *Cytherelloidea*. A. *C. newtoni*, SAM–K5574, holotype, RV, BH9 Richards Bay, 120,22 m, Santonian III, SEM 720. B. *C. newtoni*, SAM–PC6490, LV, locality 15–5, Mtubatuba, Coniacian IV, SEM 1919. C. *C. umzambaensis*, SAM–PC6491, RV, Umzamba bed 1, Santonian II, SEM 710. D. *C. umzambaensis*, SAM–PC6492, RV, locality 15–7, Mtubatuba, Coniacian IV, SEM 1953. E. *C. gardeni*, SAM–PC6493, LV, Umzamba bed 3, Santonian III, SEM 714. F. *C. gardeni*, SAM–PC6494, RV, Umzamba bed 3, Santonian III, SEM 717. Scale bars = 100 μ.

Remarks

No additional specimens of this distinctive species have been found in the Zululand outcrops. SEM photographs of Santonian II topotypic material from Umzamba are included here to supplement the inadequate original illustrations by Dingle (1969). The longitudinal rib pattern in the posterior part of the valve is very similar to that of *C. griesbachi*, but the two species have a different valve outline (*C. gardeni* is distinctly elongate), and *C. gardeni* is overall delicately reticulate.

Age and distribution

Cytherelloidea gardeni ranges Santonian II to Santonian III in the Umzamba cliff section, and one specimen was recorded in the lower part of Santonian III in the Richards Bay borehole (BH9).

Cytherelloidea griesbachi Dingle, 1980

Fig. 7B

Cytherelloidea griesbachi Dingle, 1980: 10–11, figs 3B, 4D.

Remarks

A rare species whose rib pattern has similarities with that of *C. mtubaensis*.

Age and distribution

Cytherelloidea griesbachi ranges uppermost Santonian III to Campanian II in the Richards Bay BH9 borehole. One specimen was recorded by Dingle (1980) from Santonian III at Umzamba.

Suborder PODOCOPINA Sars, 1866

Superfamily BAIRDIACEA Sars, 1888

Family **Bairdiidae** Sars, 1888

Genus *Bairdoppilata* Coryell, Sample & Jennings, 1935

Bairdoppilata andersoni Dingle, 1980

Fig. 9A–C

Bairdoppilata andersoni Dingle, 1980: 12–14, fig. 5A–F; 1981: 25–29, figs 11A–D, 13A–B.

Remarks

Specimens from Santonian Zululand outcrops have a prominent posterior beak, but can be accommodated within the intraspecific morphological variations encountered from other areas.

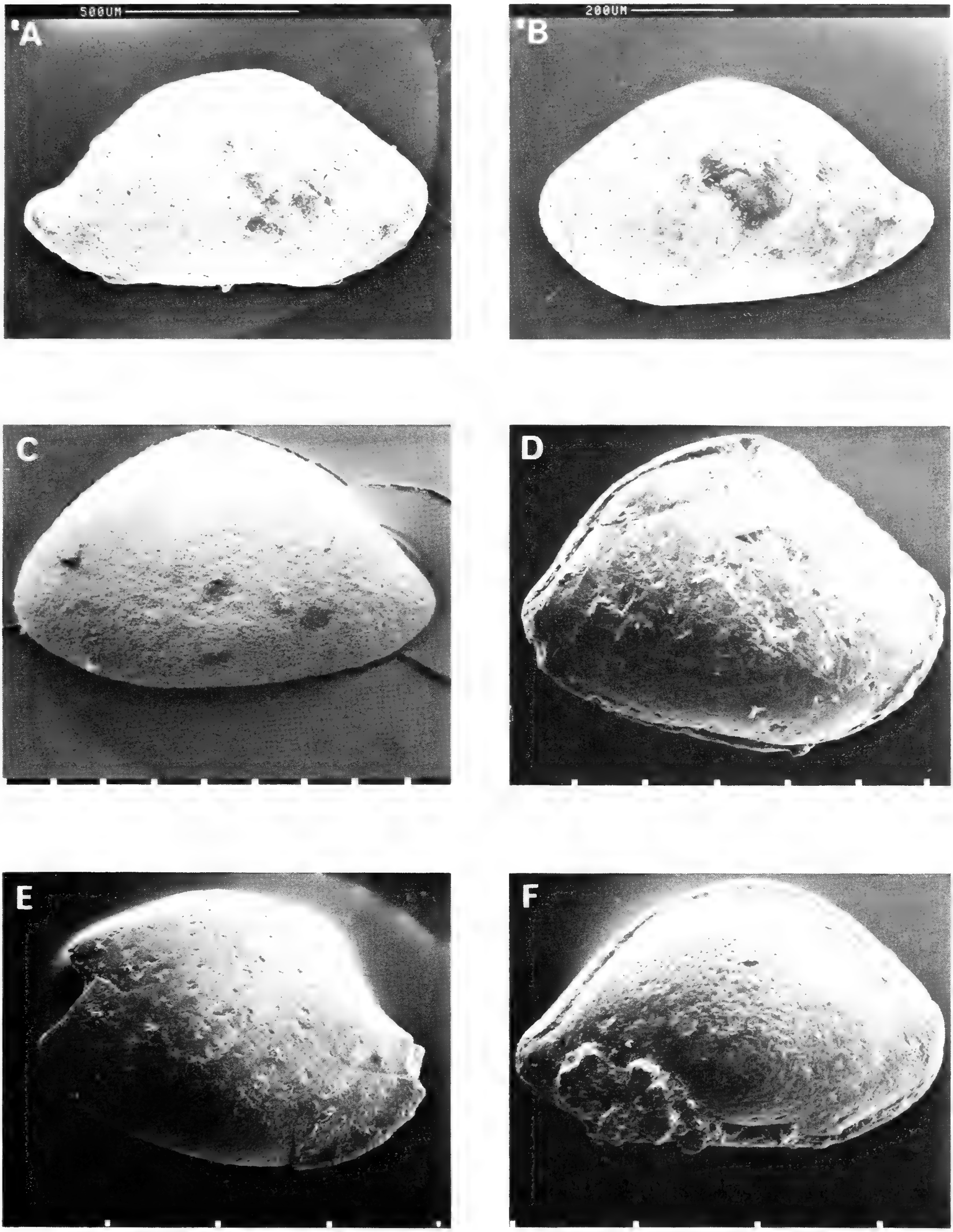


Fig. 9. Genus *Bairdoppilata*. A. *B. andersoni*, SAM–PC6495, LV, locality 74–15, Mtubatuba, Santonian III, SEM 2352. B. *B. andersoni*, SAM–PC6496, RV, BH9 Richards Bay, 139,8 m, Santonian III, SEM 2344. C. *B. andersoni*, SAM–PC6497, RV, Umzamba bed 5, Santonian III, SEM 2076. D. *Bairdoppilata* sp. 2322, SAM–PC6498, LV, J(c)–1 borehole, 1 981 m, Santonian. E. *Bairdoppilata* sp. 2327, SAM–PC6499, LV, J(c)–1 borehole, 2 152 m, Turonian, SEM 2328. F. *Bairdoppilata* sp. 2336, SAM–PC6500, LV, J(c)–1 borehole, 2 213 m, Upper Cenomanian, SEM 2335. Scale bars: A = 500 μ, B = 200 μ, C–D = 100 μ, E–F = 300 μ.

Age and distribution

Bairdoppilata andersoni is one of the temporally and spatially most widespread ostracod taxa in south-east Africa, but is numerically rare in the Santonian strata of Richards Bay, Zululand, and Umzamba. It is known to range Santonian II–Campanian II in BH9, Santonian III–Campanian I at Umzamba, Santonian III–Maastrichtian II (Zululand), and occurs in Maastrichtian III on the Agulhas Bank.

Bairdoppilata sp. 2322

Fig. 9D

Remarks

One badly worn carapace that is probably conspecific with *B.* cf. *africana*, which was illustrated by Dingle (1981, fig. 12F). *Bairdoppilata* cf. *africana* was recorded from Campanian–Maastrichtian sections of the J(c)–1 borehole.

Age and distribution

Santonian, J(c)–1 borehole, 1 981 m (6 500 ft).

Bairdoppilata sp. 2327

Fig. 9E

Remarks

A broken valve whose affinities to other members of the genus in the J(c)–1 borehole are not clear.

Age and distribution

Turonian, J(c)–1 borehole, 2 152 m (7 060 ft).

Bairdoppilata sp. 2336

Fig. 9F

Remarks

Two punctate carapaces of a species that is more elongate than *Bairdoppilata* sp. 2322 and *B.* cf. *africana*.

Age and distribution

Upper Cenomanian–Santonian, J(c)–1 borehole, 2 213 m and 1 981 m (7 260 ft and 6 500 ft).

Genus *Bythocypris* Brady, 1880

Bythocypris richardsbayensis Dingle, 1980

Fig. 10A–B

Bythocypris richardsbayensis Dingle, 1980: 14–16, fig. 6A–E; 1981: 31, fig. 14A–C.

Remarks

This species is sparsely distributed throughout the Coniacian–Santonian strata of south-east Africa, but the oldest recorded specimens show no significant morphological differences from the type specimens (Campanian), or younger material. *Bythocypris richardsbayensis* only becomes abundant in the deeper-water, post-Santonian sediments.

Age and distribution

Coniacian IV–Maastrichtian II (Zululand outcrops), Maastrichtian III (Agulhas Bank), Santonian II–Campanian II (Richards Bay borehole). So far, no specimens have been recorded from Umzamba, presumably because of the shallow-water environments that prevailed there.

Bythocypris cf. *richardsbayensis*

Fig. 10C–D

Remarks

Two carapaces (one crushed) of a species with a similar lateral outline to *B. richardsbayensis*.

Age and distribution

Upper Cenomanian–Santonian, J(c)–1 borehole, 2 213 m and 2 030 m (7 260 ft and 6 660 ft).

Superfamily CYPRIDACEA Baird, 1845

Family **Paracyprididae** Sars, 1923

Genus *Paracypris* Sars, 1866

Paracypris zululandensis Dingle, 1980

Fig. 10F

Paracypris zululandensis Dingle, 1980: 17–19, figs 7D–G, 9B; 1981: 35, fig. 16D.

Remarks

Paracypris zululandensis occurs consistently, but in small numbers, in the Coniacian and Lower Santonian strata of the Mfolozi and False Bay areas of Zululand. Dingle (1980) recorded a similar distribution in the Santonian of BH9, but noted that the species becomes relatively more abundant in the deeper-water Campanian section of the borehole.

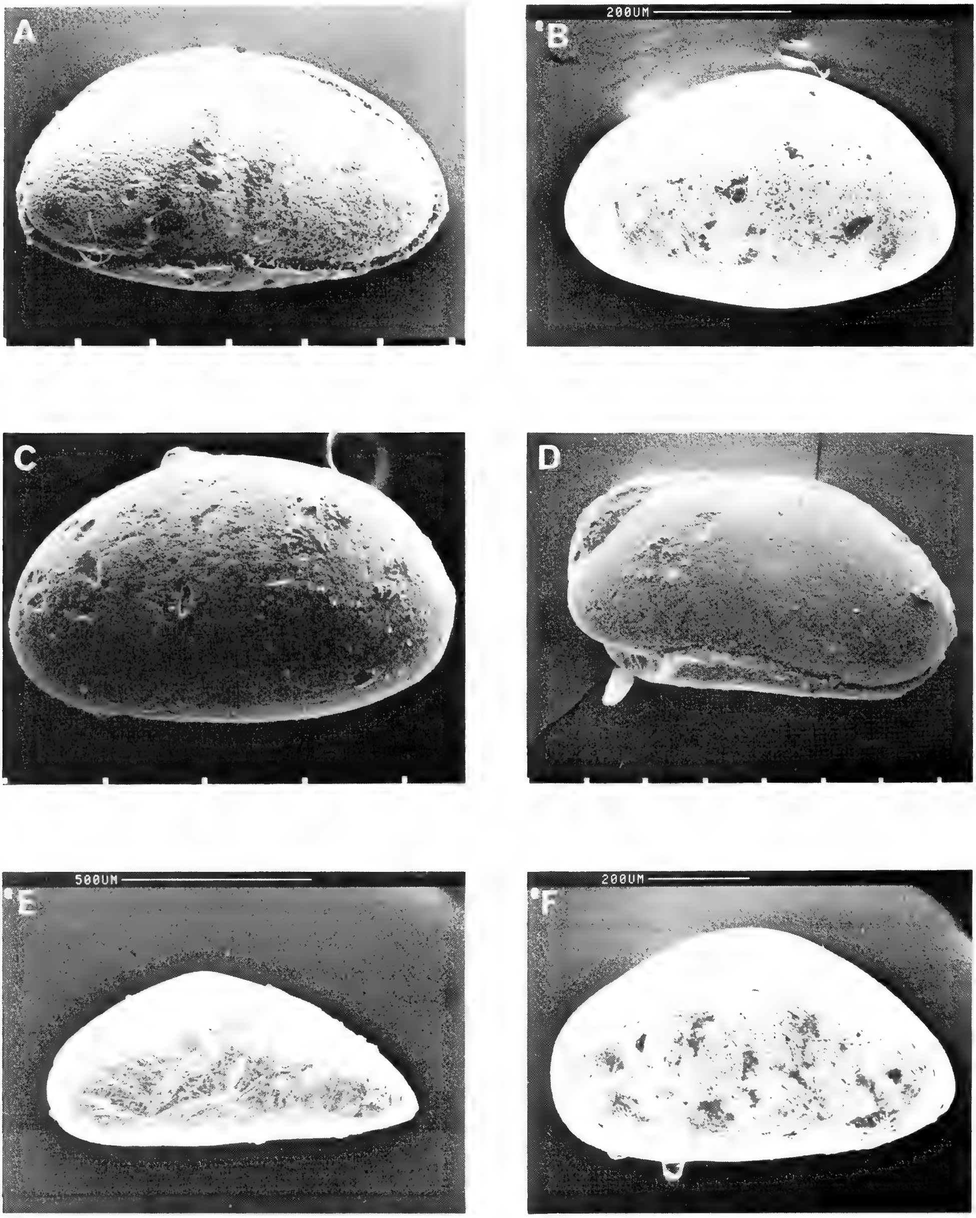


Fig. 10. A. *Bythocypris richardsbayensis*, SAM–PC6501, RV, locality 15–5, Mtubatuba, Coniacian IV, SEM 2133. B. *Bythocypris richardsbayensis*, SAM–PC6502, LV, BH9 Richards Bay, 142,0 m, Santonian III, SEM 2345. C. *Bythocypris* cf. *richardsbayensis*, SAM–PC6503, RV, J(c)–1 borehole, 2 030 m, Santonian–Coniacian, SEM 2324. D. *Bythocypris* cf. *richardsbayensis*, SAM–PC6504, RV, J(c)–1 borehole, 2 213 m, Upper Cenomanian, SEM 2337. E. *Paracypris umzambaensis*, SAM–PC6506, RV, locality 74–11/2, False Bay, Santonian II–III, SEM 2354. F. *Paracypris zululandensis*, SAM–PC6505, RV, locality 74–11/2, False Bay, Santonian II–III, SEM 2348. Scale bars: A, C, D = 100 μ, B, F = 200 μ, E = 500 μ.

Age and distribution

Coniacian IV to ?Maastrichtian I at outcrop in Zululand (Mfolozi and False Bay), Santonian II to Campanian II in the Richards Bay borehole, and Maastrichtian III, Agulhas Bank. Not found at Umzamba.

Paracypris umzambaensis Dingle, 1969

Fig. 10E

Macrocypris simplex (*non* Chapman, 1898) Chapman, 1904: 233, pl. 29 (fig. 22).
Paracypris? umzambaensis Dingle, 1969: 354–356, fig. 5.
Paracypris umzambaensis Dingle, 1980: 17, figs 7A–C, 9A; 1981: 34–35, fig. 16A–C.

Remarks

Paracypris umzambaensis occurs sporadically in the False Bay area, but becomes more abundant farther south, where it is consistently present in small numbers throughout the Richards Bay borehole, and at Umzamba. At the latter locality, it occurs to the exclusion of its close relative *P. zululandensis*. Dingle (1981) suggested that *P. umzambaensis* was more tolerant of deep-water conditions than *P. zululandensis*.

Age and distribution

Santonian III to Maastrichtian II at outcrop in Zululand (False Bay), Santonian II to Campanian II in BH9, Santonian II–III at Umzamba, and late Campanian–early Maastrichtian at Igoda (near East London).

Superfamily CYTHERACEA Baird, 1850

Family **Cytherideidae** Sars, 1925

Genus *Pondoina* Dingle, 1969

Two species of this genus have been recognized in southern Africa: *P. sulcata* (Santonian) and *P. igodaensis* (late Campanian–early Maastrichtian), whilst Krömmelbein (1972) recorded *?Pondoina* sp. from the Turonian Sibang Formation of Gabon, and the ?Coniacian Macau Formation of north-east Brazil. This suggests a Turonian to late Campanian–early Maastrichtian range for the genus. No species referable to the genus was recorded from the Turonian to Maastrichtian of Tanzania by Bate & Bayliss (1969). A link might have been expected in view of the close similarity in some other species between south-east Africa and Tanzania.

Pondoina sulcata Dingle, 1969

Fig. 11A–F

Pondoina sulcata Dingle, 1969: 356–358, fig. 6; 1980: 20, fig. 9C.

Remarks

SEM photographs of topotypic specimens are included here to supplement the original description. In particular, attention is drawn to the strongly

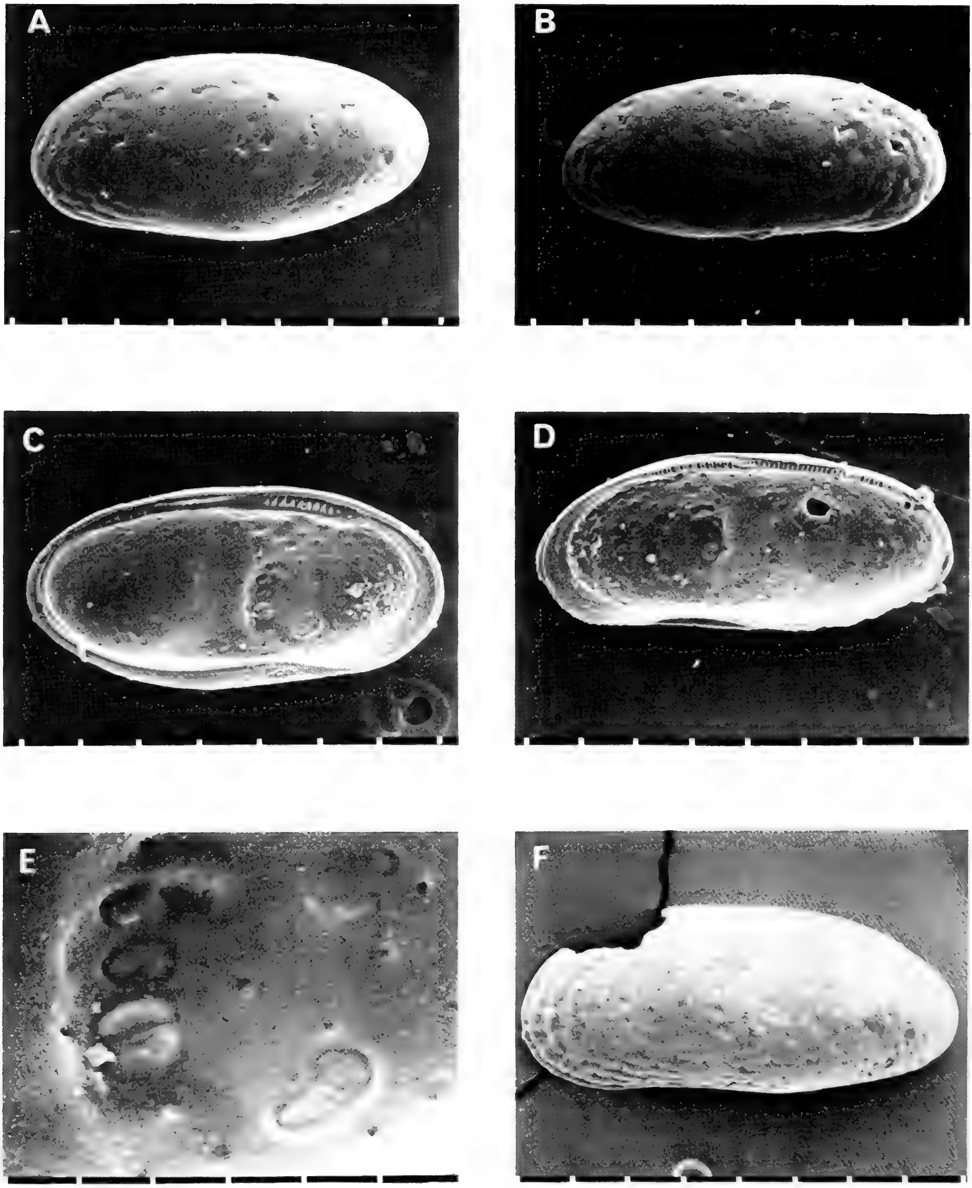


Fig. 11. *Pondoina sulcata*, Umzamba, Santonian III. A. SAM–PC6507, LV, bed 3, SEM 570. B. SAM–PC6508, RV, bed 3, SEM 572. C. SAM–PC6509, internal LV, bed 3, SEM 561. D. SAM–PC6510, internal RV, bed 3, SEM 554. E. SAM–PC6509, muscle scars, LV, bed 3, SEM 569. F. SAM–PC6511, bed 7, SEM 2086.
Scale bars: A–D, F = 100 μ, E = 30 μ.

antimerodont hinge, difference in lateral outline between LV and RV, and the MS (which has a distinctive 'clover-leaf' arrangement of the dorsal two elements of the adductors, and the divided antennal scar).

Age and distribution

Pondoina sulcata ranges Santonian II to Santonian III in its type section at Umzamba, and occurs in small numbers in the lower part of Santonian III in the Richards Bay borehole.

Family **Schizocytheridae** Mandelstam, 1960

Genus *Amphicytherura* Butler & Jones, 1957

Amphicytherura tumida Dingle, 1969

Fig. 12A–E

Amphicytherura (Amphicytherura) tumida Dingle, 1969: 368–370, fig. 13; 1980: 20–21, fig. 10A–F; 1981: 49–50, figs 23C, 25A.

Remarks

This species has not been found at outcrop in Zululand, although it is relatively common in BH9 and at Umzamba, where it can be used as a zone fossil at the top of Santonian III. Some specimens from Santonian III at Umzamba have a slightly extended AM outline compared to the topotypic material in Santonian II.

Age and distribution

Santonian II–Campanian I at Umzamba and Richards Bay borehole.

Genus *Apateloschizocythere* Bate, 1972

Apateloschizocythere? cf. *mclachlani* Dingle, 1981

Fig. 12F

?Amphicytherura sp. Dingle, 1971*b*: 404–405, fig. 7.

Remarks

The five small and poorly preserved specimens recorded by Dingle (1971*b*) have been photographed with SEM. Although generic assignment is still uncertain, they are very similar to a species described by Dingle (1981: 54–57, fig. 26A–B) from the Campanian III of Zululand. The genus has also been recorded from the Maastrichtian III of the Agulhas Bank (*Apateloschizocythere laminata* (Dingle, 1971*b*)).

Age and distribution

Lower Coniacian, sample TBD 510, Alphard Formation, Agulhas Bank.

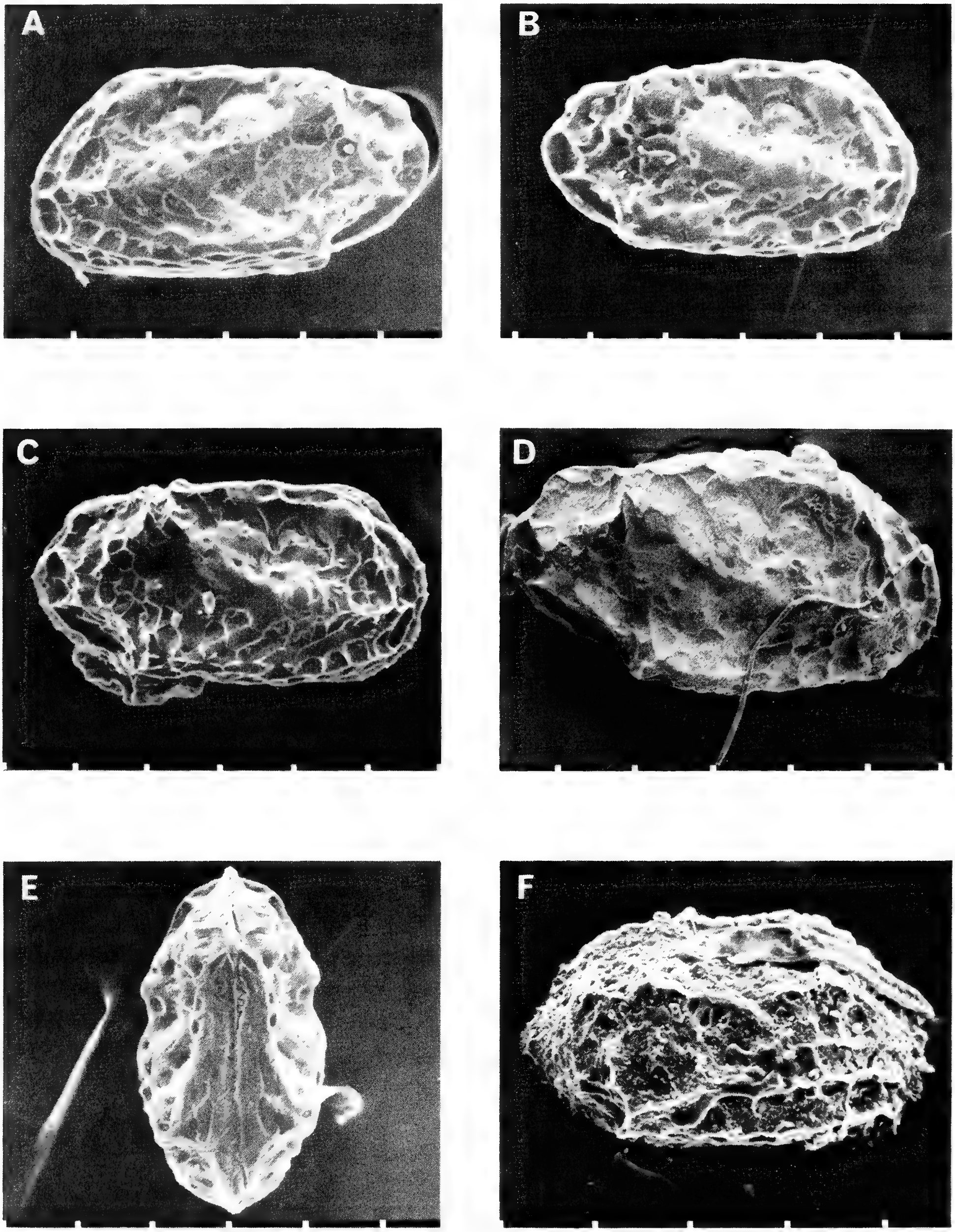


Fig. 12. A–E. *Amphicytherura tumida*. A. SAM–PC6512, LV, Umzamba bed 3, Santonian III, SEM 295. B. SAM–PC6513, RV, Umzamba bed 3, Santonian III, SEM 298. C. SAM–K5594, RV, BH9 Richards Bay, 125,0 m, Santonian III, SEM 317. D. SAM–PC6514, RV, Umzamba bed 3, Santonian III, SEM 2059. E. SAM–PC6515, carapace, dorsal view, Umzamba bed 3, Santonian III, SEM 299.
F. *Apateloschizocythere?* cf. *mclachlani* SAM–PC6516, RV, TBD 510, Agulhas Bank, Alphard Formation, Lower Coniacian, SEM 1882.
Scale bars = 100 μ.

Genus *Cnestocythere* Triebel, 1950

Cnestocythere? sp. 2091

Fig. 13A–B

?Cnestocythere sp. Dingle, 1969: 370–371, fig. 14.

Remarks

This specimen was illustrated by Dingle (1969), but SEM photographs show the hinge to be damaged, so that it may not originally have been merodont. This casts further doubt upon its generic placement. No further specimens of this species have been recovered. An SAM serial number (PC6517) has been allocated to the original specimen, which supersedes UCT number MG–1–2–10.

Age and distribution

Santonian III, Umzamba.

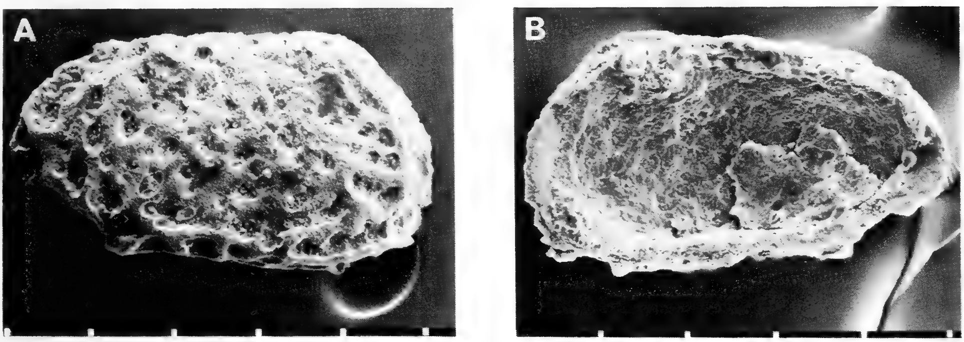


Fig. 13. *Cnestocythere?* sp. 2091, SAM–PC6517, Umzamba bed 3, Santonian III. A. External RV, SEM 2091. B. Internal RV, SEM 2155. Scale bars = 100 μ.

Family **Brachycytheridae** Puri, 1954

Genus *Brachycythere* Alexander, 1933

Brachycythere is one of the key genera for an understanding of the routes and timing of ostracod population movements from the Equatorial Atlantic into the South Gondwana province after the mid-Cretaceous hiatus. In southern Africa, five species have been recognized: two appear in the Coniacian (*B. longicaudata* and *B. agulhasensis*); and three appear in the Santonian (*B. sicarius, B. pondolandensis*, and *B. rotunda*).

Fourteen species of *Brachycythere* have so far been recorded from Africa, and a further seven from nearby areas in the Middle East. Their ranges have been plotted in Table 6, outlines of holotypes and topotypes are illustrated in Figure 14, and their length/height scattergrams are shown in Figure 15. The earliest records are in Cenomanian strata: *B.* cf. *sapucariensis* (Tunisia—Bismuth *et al.* 1981); *B.* gr. *sapucariensis* (Gabon—Grosdidier 1979); *B. sapucariensis* by Schaller (1969, reported in Reyment 1980*a*) from north-east Brazil; and *B.* aff. *ekpo* (Morocco—Oertli 1963). *Brachycythere sapucariensis* and closely related forms have been widely reported from north-east Brazil and various localities in equatorial, west and north Africa, as far east as Tunisia, and range into the Coniacian. As will be discussed below, it is closely related to the main southern African species (*B. longicaudata*). The only other widely reported species is *B. angulata* from Egypt (Turonian), Nigeria (Coniacian), Senegal and Lebanon (Coniacian–Santonian), Cameroon (Santonian), and Israel (Santonian to Maastrichtian).

For the present investigation, it is important to note that the genus *Brachycythere* was well represented in the Equatorial Atlantic and North Africa (probably five species) by Cenomanian–early Turonian times, but that no species of the genus occur in southern Africa or any other South Gondwana locality before the local mid-Cretaceous non-sequence. This hiatus locally ranges in age from late Cenomanian to late Turonian or early Coniacian.

Brachycythere longicaudata (Chapman, 1904)

Figs 16A–D, 17A–D

Cytheridea longicaudata Chapman, 1904: 234–235, pl. 39 (fig. 21). Howe & Laurencich, 1958: 279.

Cythere ?drupracea (*non* Jones, 1884) Chapman, 1904: 234.

Brachycythere longicaudata (Chapman) Dingle, 1969: 358–361, fig. 7; 1980: 25–26, figs 12A–C, 13A–D; 1981: 71–72, fig. 34B–C.

Brachycythere aff. *sapucariensis* Krömmelbein, 1964, Bate, 1969, in Bate & Bayliss: 137–138, 164, pl. 7 (fig. 1) (*partim* (BMNH Io790)).

Remarks

Specimens collected from Coniacian outcrops in Zululand plot within the overall species field on a length/height scattergram, but overlap the subfields of Santonian and Campanian–Maastrichtian material (Fig. 15). This distribution illustrates one aspect of the considerable intraspecific morphological variation that is apparent within the species *B. longicaudata*: generally Santonian specimens are larger and more elongate, whereas the Campanian–Maastrichtian individuals are smaller and somewhat squatter. The new Coniacian samples suggest that the earliest representatives were similar in character to the Campanian varieties and that environmental conditions during Santonian times were favoured by larger and more elongate varieties. Although individuals within the overall Coniacian to Maastrichtian populations could be assigned to separate

TABLE 6

Temporal distribution of the genus *Brachycythere* in Cretaceous strata of Africa and surrounding areas.

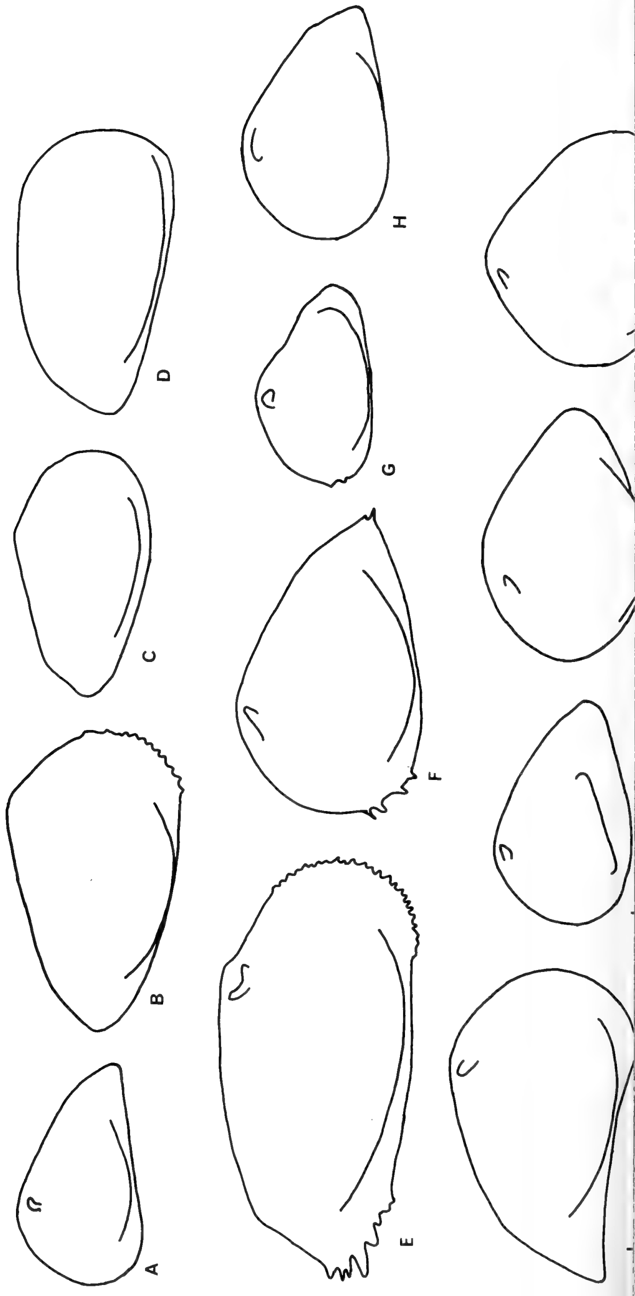
Species	Reference	Locality	Cen.			Tur.		Coniacian					Santon.			Campanian					Maastr.		
			L	M	U	L	U	I	II	III	IV	V	I	II	III	I	II	III	IV	V	I	II	III
gr. *sapucariensis*	Krömmelbein, 1964	G, T, B	—	—	—	—	—	—															
aff. *ekpo*	Oertli (1963)	M	—	—	—																		
ledaforma	Masoli (1966)	M			—	—																	
gr. *angulata*	Grekoff, 1951	A, L, C, S, E, Is				—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
dumoni	Bismuth & St. Marc, 1981*	T				—																	
longicaudata	This paper	SA, Tz					—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
agulhasensis	Dingle, 1971*b*	SA						—	—														
ekpo	Reyment, 1960	N, E, Is						—	—	—	—	—	—	—	—	—							
IRC 28	Grosdidier, 1973	I											—	—	—	—							
IRH 34	Grosdidier, 1973	I											—	—									
IRE 10	Grosdidier, 1973	I											—										
IRJ 9	Grosdidier, 1973	I											—										
IRJ 10	Grosdidier, 1973	I											—										
sicarius	Dingle, 1980	SA												—	—	—	—	—	—	—	—		
pondolandensis	Dingle, 1969	SA												—	—								
rotunda	Dingle, 1969	SA												—									
IRE 5	Grosdidier, 1973	I													—	—	—	—	—	—			
beershevaensis	Honigstein, 1983	Is														—	—						
kulatturensis	Guha, 1971	In																			—	—	—
gr. *carinata*	Gowda, 1966	In																			—	—	—
armata	Reyment, 1960	N																				—	—
oguni	Reyment, 1960	N																				—	—
sp. indet	Reyment, 1960	N																					—

Notes:

1. *Brachycythere* gr. *sapucariensis* includes cf., aff., as described by: Grosdidier (1979), Bismuth *et al.* (1981), Krömmelbein (1976), Neufville (1973), Reyment (1960).
2. *Brachycythere* gr. *angulata* includes aff.,?, as described by: Grekoff (1951, 1969), Reyment (1960), Apostolescu (1963), Van den Bold (1964), Damotte & St. Marc (1972), Honigstein (1983).
3. *Brachycythere longicaudata* includes Bate (1969).
4. *Brachycythere ekpo* includes cf. Van den Bold (1964), Honigstein (1983).

* = in Bismuth *et al.* 1981.

Abbreviations:
A = Algeria, B = Brazil, C = Cameroon, E = Egypt, G = Gabon, I = Iran, In = India, Is = Israel, L = Lebanon, M = Morocco, N = Nigeria, S = Senegal, SA = South Africa, T = Tunisia, Tz = Tanzania.


A
B
C
D
E
F
G
H

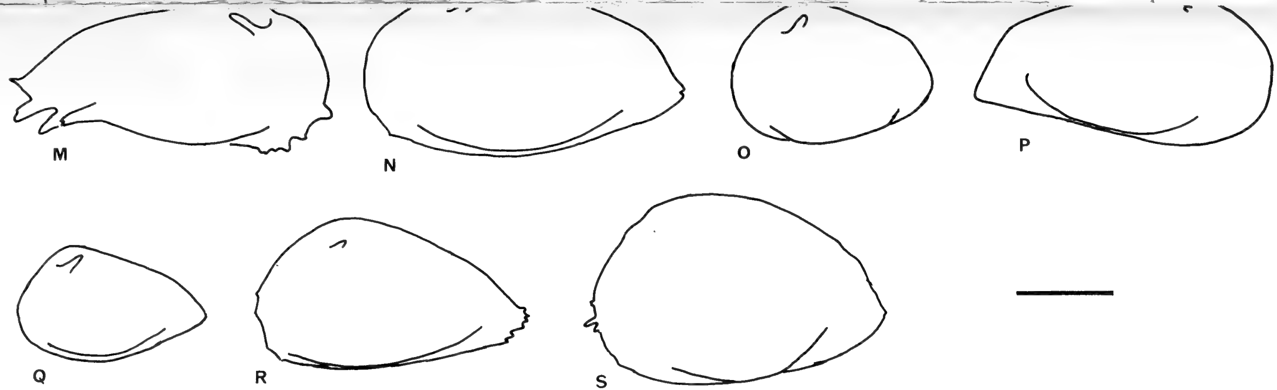


Fig. 14. Comparative outlines of type specimens of *Brachycythere* species from the middle and late Cretaceous of Africa and adjacent areas. See Table 6 for ranges and authorship.
A = *B. sapucariensis*, B = *B. ledaforma*, C = *B. angulata*, D = *B. dumoni*, E = *B. longicaudata*, F = *B. agulhasensis*, G = *B. ekpo*, H = *Brachycythere* IR C28, I = *Brachycythere* IR H34, J = *Brachycythere* IR E10, K = *Brachycythere* IR J9, L = *Brachycythere* IR J10, M = *B. sicarius*, N = *B. pondolandensis*, O = *B. rotunda*, P = *Brachycythere* IR E5, Q = *B. kulatturensis* (not to scale), R = *B. armata*, S = *B. oguni*.
Scale bar = 300 μ.

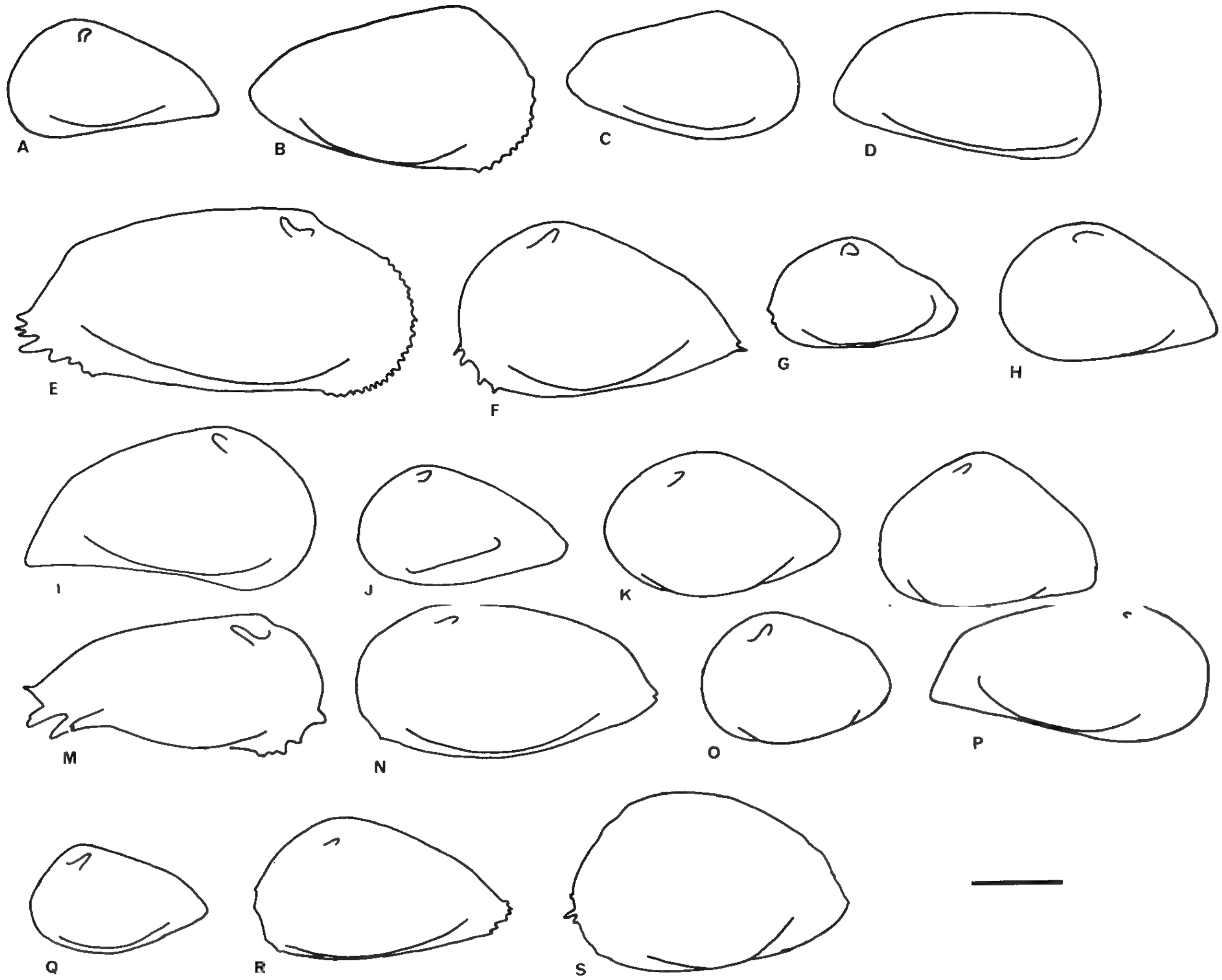


Fig. 14. Comparative outlines of type specimens of *Brachycythere* species from the middle and late Cretaceous of Africa and adjacent areas. See Table 6 for ranges and authorship.
A = *B. sapucariensis*, B = *B. ledaforma*, C = *B. angulata*, D = *B. dumoni*, E = *B. longicaudata*, F = *B. agulhasensis*, G = *B. ekpo*, H = *Brachycythere* IR C28, I = *Brachycythere* IR H34, J = *Brachycythere* IR E10, K = *Brachycythere* IR J9, L = *Brachycythere* IR J10, M = *B. sicarius*, N = *B. pondolandensis*, O = *B. rotunda*, P = *Brachycythere* IR E5, Q = *B. kulatturensis* (not to scale), R = *B. armata*, S = *B. oguni*.
Scale bar = 300 μ.

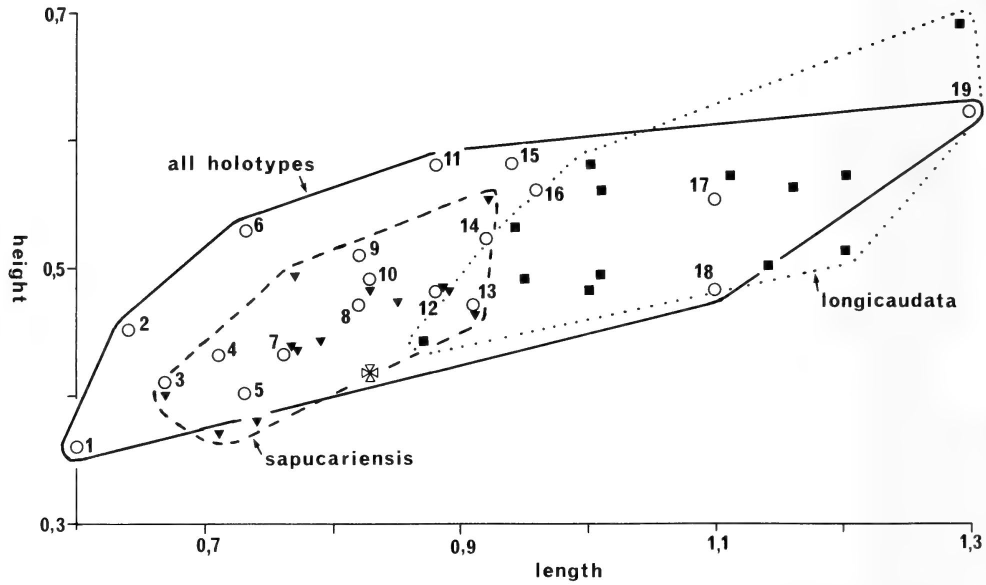


Fig. 15. Length/height scattergram (in mm) of specimens of *Brachycythere*. Solid line and circles = type specimens from the middle and late Cretaceous of Africa and adjacent areas; dashed line and triangles = specimens of *B. sapucariensis* reported in the literature; maltese cross = specimens reported as *B.* aff. *sapucariensis* by Bate & Bayliss (1969).
Key to species: 1 = *B. ekpo*, 2 = *B. rotunda*, 3 = *Brachycythere* IR E10, 4 = *Brachycythere* IR C28, 5 = *B. angulata*, 6 = *Brachycythere* IR J10, 7 = *B. sapucariensis*, 8 = *B. armata*, 9 = *B. kulatturensis*, 10 = *Brachycythere* IR J9, 11 = *B. oguni*, 12 = *B. dumoni*, 13 = *Brachycythere* IR E5, 14 = *B. ledaformis* (as reported by Masoli (1966)), 15 = *B. agulhasensis*, 16 = *Brachycythere* IR H34, 17 = *B. pondolandensis*, 18 = *B. sicarius*, 19 = *B. longicaudata*.

morphotypes on the grounds of lateral outline, such subdividsion has been found impractical because the bulk of the populations would then fall into intermediate categories. In terms of lateral outline (regardless of valve size) this poses problems in discriminating *B. longicaudata* from certain other species, notably *B. sapucariensis*.

On a length/height scattergram of holotypic (and neotypic) specimens of *Brachycythere* from Africa and adjacent areas, the types of *B. longicaudata* and *B. sapucariensis* are widely separated, and in lateral outline are clearly differentiated (Fig. 17). This distinction is also seen in other points of morphological difference: curvature of AM, shape of VM, shape and spinosity of posteroventral area. The two types are Santonian and Coniacian age, respectively. However, several other workers have reported Krömmelbein's Brazilian species from localities in west and north Africa, and if representatives of these materials are compared in shape (but not size) to the general population of *B. longicaudata*, the distinctions become blurred. On a length/height scattergram the *B. sapucariensis*-related specimens plot to the left of the *B. longicaudata* populations and in comparison with other *Brachycythere* type specimens their

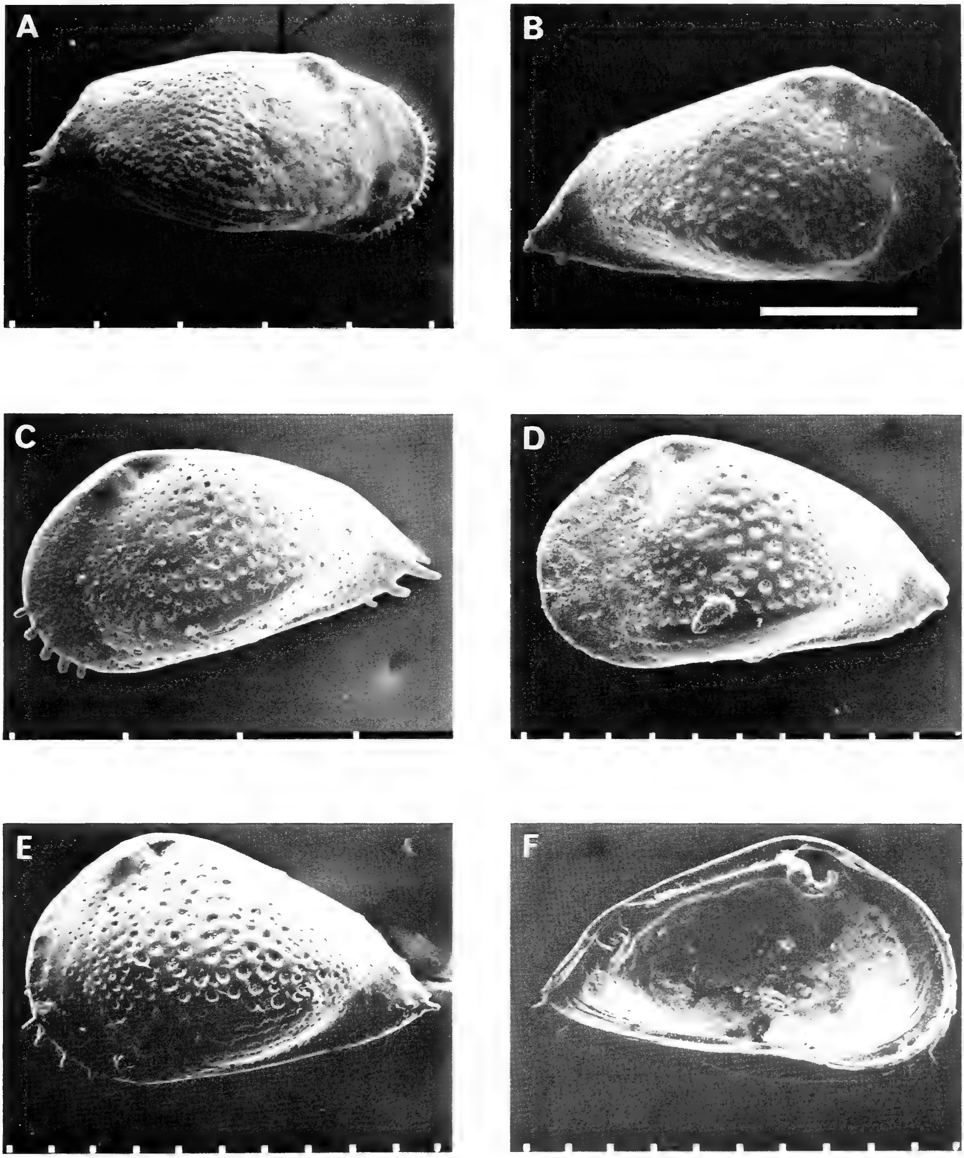


Fig. 16. A–D. *Brachycythere longicaudata*. A. SAM–PC6518, neotype, RV, Umzamba bed 1, Santonian II, SEM 2089. B. BMNH Io790, RV, Wami River area, Luzangazi Stream, Tanzania, Upper Turonian, SP7/848. C. SAM–PC6519, LV, locality 16–1, Mtubatuba, Coniacian III, SEM 1939. D. SAM–PC6520, LV, locality 15–5, Mtubatuba, Coniacian IV, SEM 1922. E–F. *Brachycythere agulhasensis*, TBD 510, Agulhas Bank, Alphard Formation, Lower Coniacian. E. SAM–PC6522, holotype, LV, SEM 1806. F. SAM–PC6542, internal LV, SEM 1807. Scale bars: A–C = 300 μ, D–F = 100 μ.

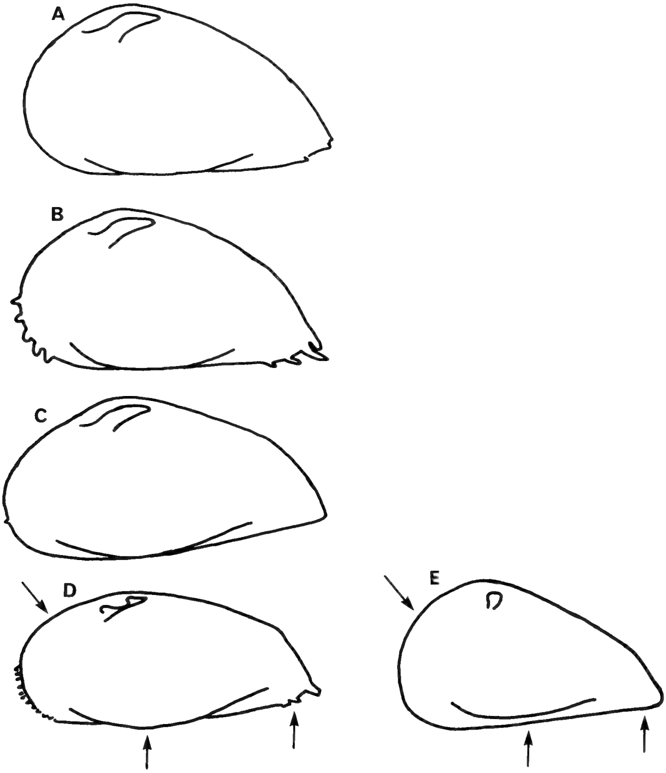


Fig. 17. Outline of *Brachycythere* species, LV. A–D. *B. longicaudata*. A. SAM–PC6520, locality 15–5, Mtubatuba, Coniacian IV, SEM 1922. B. SAM–PC6519, locality 16–1, Mtubatuba, Coniacian III, SEM 1939. C. SAM–K5604, BH9 Richards Bay, 92,27 m, Campanian I, SEM 549. D. SAM–PC6521, Umzamba bed 3, Santonian III, SEM 534. E. *B. sapucariensis*, SMF Xe2990, holotype, Aracaju, Brazil, Coniacian. Arrowed locations show significant differences in lateral outline between *B. longicaudata* and *B. sapucariensis*.

field includes the holotypes of *B. angulata* Grekoff, *B. armata* Reyment, *B. kulatturensis* Guha, and *B. dumoni* Bismuth & St. Marc, as well as several of the morphotypes recorded by Grosdidier (1979) from Iran. At this stage, with the exception of the topotypic material illustrated by Krömmelbein (1964), no consistent subdivision can be made between many members of the two populations other than one based on overall size.

Bate (*in* Bate & Bayliss 1969) recorded *B.* aff. *sapucariensis* from the Upper Turonian of Tanzania. In the subsequent discussion to this paper, Bate (p. 164) compares his specimen more closely with *B. longicaudata*. An SEM photograph of the more elongate specimen recorded by Bate (BMNH Io790) (Fig. 16B) confirms this closeness, and I regard this as the earliest record of Chapman's species.

Age and distribution

The uncertainty engendered by the apparent wide intraspecific morphological variations within *B. sapucariensis* and *B. longicaudata* make temporal and spatial ranges difficult to assign. The type specimens come from the Coniacian Sapucari Formation, eastern Brazil, and Santonian II at Umzamba, respectively. It should be noted that Krömmelbein (1964) originally considered the Brazilian material to be Lower Turonian in age, but has since revised his estimate to Coniacian (?Lower) (Krömmelbein 1976: 543–544).

Taken at face value, the reported distribution of *B. sapucariensis* is Lower Cenomanian to ?Lower Coniacian, with the earliest records from Gabon and Morocco. *Brachycythere longicaudata* has its earliest record in the Upper Turonian of Tanzania, and in southern Africa is known to range Coniacian III (locality 16–1, Mtubatuba) to Maastrichtian II (Nibela) in Zululand, and farther south an incomplete range of Santonian II to Campanian I is recorded at Umzamba. It occurs in the late Campanian–early Maastrichtian at Igoda. The species has not been recorded from the Agulhas Bank (although no Santonian or Campanian faunas have yet been described from this area).

Brachycythere agulhasensis Dingle, 1971

Figs 16E–F, 18A

Brachycythere agulhasensis Dingle, 1971*b*: 399–400, fig. 3.

Remarks

No further specimens of this species have been encountered. SEM photographs of the holotype are included here, and some of the points on which *B. agulhasensis* differs from *B. longicaudata* are emphasized: it has a shorter, but more massive hinge with a particularly deep, rounded ATE, a coarsely crenulate ME, and a relatively short, high PTE; a coarse surface reticulation, and a relatively low length/height ratio (1,61 cf. mean 2,02 for all specimens of *B. longicaudata* plotted on Figure 15). The holotype, originally designated MG–2–1–25, has been transferred to the South African Museum under the number SAM–PC6522.

Age and distribution

Brachycythere agulhasensis is known only from the Lower Coniacian Alphard Formation of the Agulhas Bank (sample TBD 510).

Brachycythere sicarius Dingle, 1980

Fig. 18B

Brachycythere sicarius Dingle, 1980: 27–29, figs 13F, 14A–F; 1981: 72–73, fig. 35A.

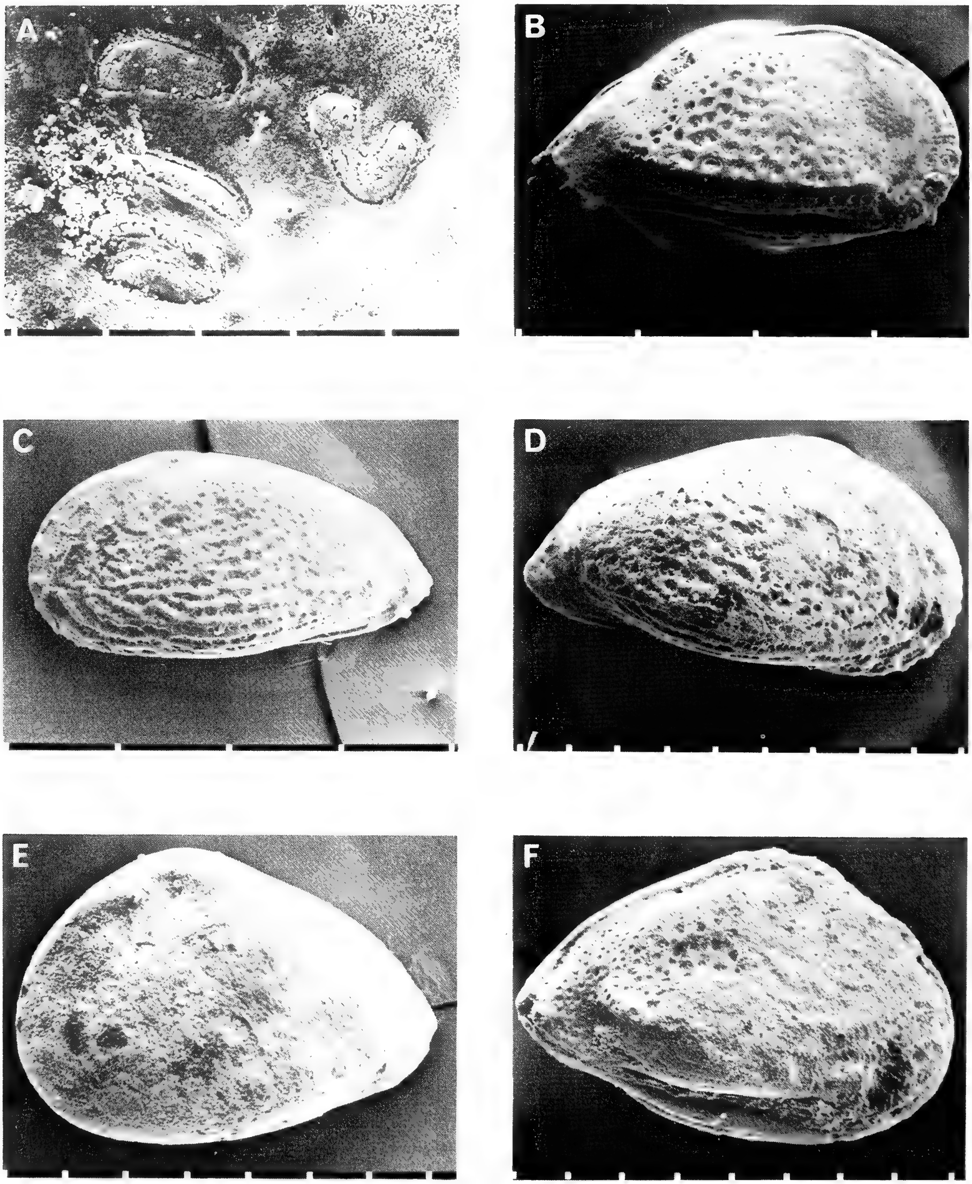


Fig. 18. *Brachycythere*. A. *B. agulhasensis*, SAM–PC6522, holotype, MS, LV, TBD 510, Agulhas Bank, Alphard Formation, Lower Coniacian, SEM 1809. B. *B. sicarius*, SAM–PC6523, RV, Umzamba bed 3, Santonian III, SEM 2058. C. *B. pondolandensis*, SAM–PC6524, holotype, LV, Umzamba bed 1, Santonian II, SEM 2112. D. *B. pondolandensis*, SAM–PC6525, RV, Umzamba bed 1, Santonian II, SEM 2115. E. *B. rotunda*, SAM–PC6526, holotype, LV, Umzamba bed 1, Santonian II, SEM 2092. F. *B. rotunda*, SAM–PC6527, RV, Umzamba bed 1B, Santonian II, SEM 2049.
Scale bars: A = 30 μ, B–C = 300 μ, D–F = 100 μ.

Remarks

Morphological similarities suggest that *B. sicarius* evolved from *B. longicaudata* in early Santonian times. It shows a similar range of intraspecific variations to its progenitor, in addition to which the earliest populations suggest that, as in the case of *B. longicaudata*, they lie at the elongate end of the length/height scattergram.

Age and distribution

Santonian II (Richards Bay BH9 borehole) to Maastrichtian I (outcrops) in Zululand, and Santonian III at Umzamba.

Brachycythere pondolandensis Dingle, 1969

Figs 18C–D, 19

Brachycythere pondolandensis Dingle, 1969: 361–362, fig. 8.

Remarks

The holotype and one paratype are re-illustrated here with SEM photographs, which emphasize the fine ribbing and foveolate-like ornamentation of the anterior and posterior regions of this distinctive, but rare, species. The MS pattern is unusual in having a subdivided top scar in the adductor set (Fig. 19). New numbers have been allocated to the re-illustrated specimens following their transfer to the South African Museum: holotype (MG–1–1–6) = SAM–PC6524; paratype (MG–1–1–8) = SAM–PC6525.

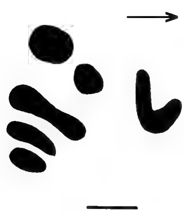


Fig. 19. Muscle scars of *Brachycythere pondolandensis*, SAM–PC6581, LV, Umzamba bed 3, Santonian III, SEM 529. Scale bar = 30 μ.

Age and distribution

Brachycythere pondolandensis has a restricted range in time and space: it occurs in Santonian II and III strata only at Umzamba and Richards Bay BH9 borehole. No specimens were recovered from the Santonian locality 74 (False Bay), but as noted previously (Dingle 1980), the species appears to be particularly susceptible to decalcification and is often poorly preserved in otherwise

well-preserved faunas. Potentially, *B. pondolandensis* is a good Santonian zone fossil for south-east Africa south of 29°S.

Brachycythere rotunda Dingle, 1969

Fig. 18E–F

Brachycythere rotunda Dingle, 1969: 362–363, fig. 9.

Remarks

SEM stereopairs of the holotype show it to have a shallow longitudinal median depression in the vicinity of mid-length, a faint, coarse, widely-spaced reticulate ornamentation in a posteromedian position, a deep circular ocular depression flanked posteriorly by a lateral cheek, and a marked, almost alate upswing of the VM at its posterior extremity. A relatively well-preserved specimen from the lowest Santonian beds at Umzamba is also assigned to the species. It has a coarse reticulate ornament in the posterior area, and a median longitudinal depression. In Figure 15, *B. rotunda* plots to the left-hand side of the length/height scattergram, where it is well displaced from the *B. longicaudata* field, and lies closest to the types of *B. ekpo* and *Brachycythere* sp. IR E10. The holotype, originally designated MG–1–2–2, has been transferred to the South African Museum under the number SAM–PC6526.

Age and distribution

Brachycythere rotunda is rare and is known only from the Santonian II at Umzamba.

Family **Collisarborisidae** Neale, 1975

Genus *Paraphysocythere* Dingle, 1969

Paraphysocythere thompsoni Dingle, 1969

Fig. 20A–C

Paraphysocythere thompsoni Dingle, 1969: 365–366, fig. 11.

Remarks

SEM photographs of topotypic material are included here to supplement the original descriptions. In particular, attention is drawn to the delicate rib pattern in the anterior area and the overall fine intercostal reticulation.

Age and distribution

Although additional material has been collected since Dingle's (1969) original records, neither the spatial nor temporal range of this species has been extended. It is known only from the Santonian II to III of Umzamba. This distribution suggests that it may be a good zone fossil for Santonian strata in south-east Africa south of about 31°S.

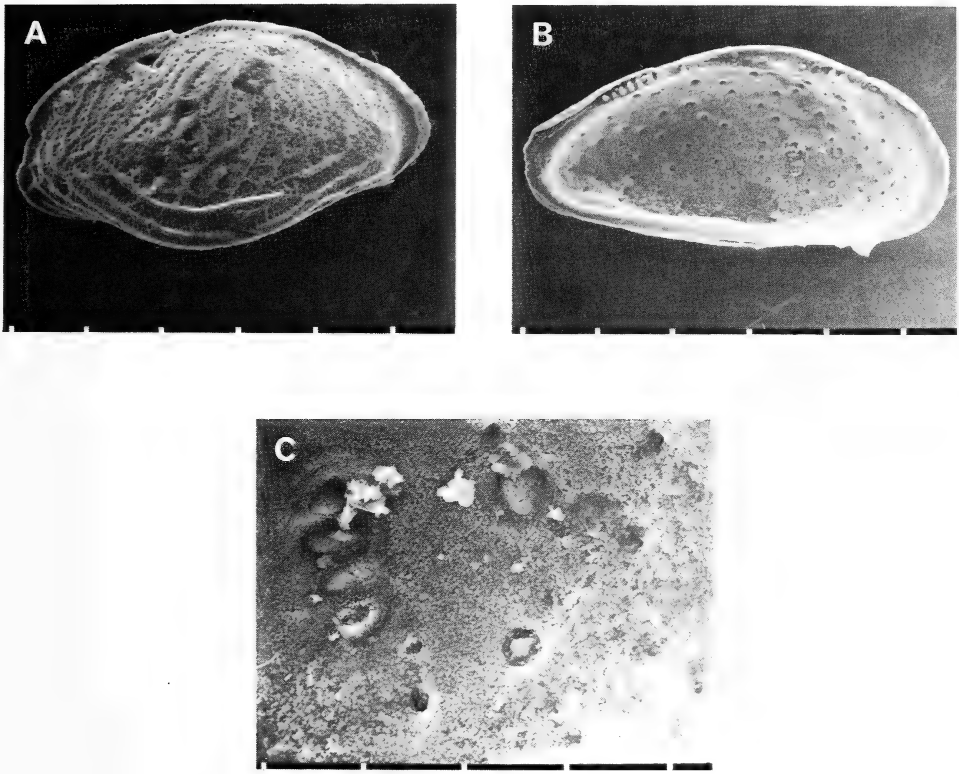


Fig. 20. *Paraphysocythere thompsoni*, Umzamba bed 3, Santonian III. A. SAM–PC6528, LV, SEM 479. B–C. SAM–PC6529, LV. B. Internal view, SEM 480. C. MS, SEM 482. Scale bars: A–B = 100 μ, C = 30 μ.

Family **Progonocytheridae** Sylvester-Bradley, 1948

Subfamily Protocytherinae Lubimova, 1955

Genus *Veenia* Butler & Jones, 1957

Veenia obesa Dingle, 1969

Fig. 21A–F

Veenia obesa Dingle, 1969: 366–368, fig. 12.

Remarks

Despite extensive collecting, no specimens of this distinctive species have been recorded in Zululand at outcrop or in the Richards Bay BH9 borehole. Some of the type material used by Dingle (1969), as well as additional specimens collected from Umzamba during the present study are illustrated here. SEM photographs show that the ATE in RV is somewhat more pointed than originally

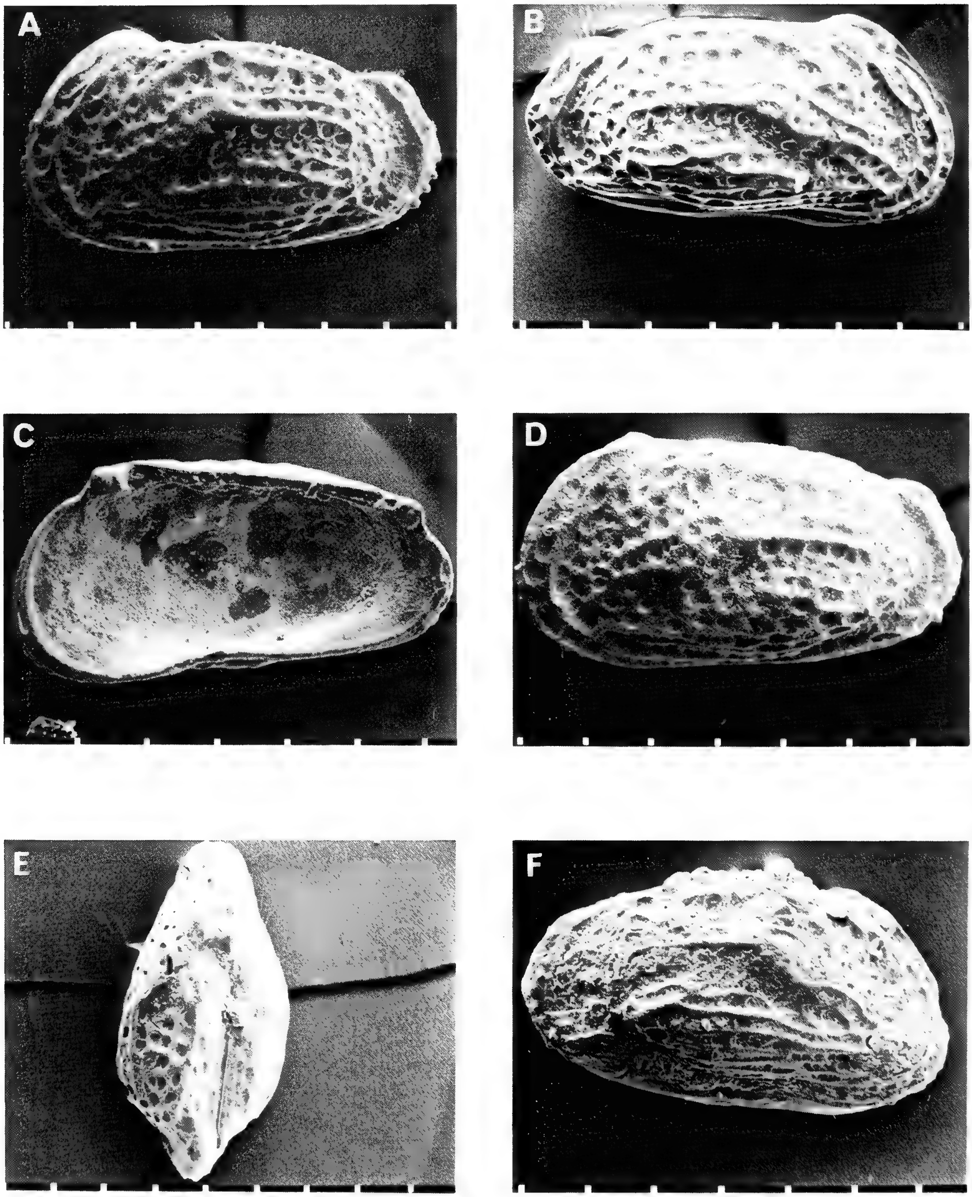


Fig. 21. *Veenia obesa*. A. SAM–PC6530, holotype, LV, Umzamba bed 1, Santonian II, SEM 2095. B. SAM–PC6531, RV, Umzamba bed 1, Santonian II, SEM 2100. C. SAM–PC6532, internal view, RV, Umzamba bed 1, Santonian II, SEM 2097. D. SAM–PC6533, LV, Umzamba bed 5, Santonian III, SEM 2070. E. SAM–PC6534, carapace, dorsal view, Umzamba bed 5, Santonian III, SEM 2071. F. SAM–PC6535, LV, Umzamba bed 1B, Santonian II, SEM 2051. Scale bars = 100 μ.

illustrated, but that the reference to a 'crenulate groove' as the LV ME is unproven and may be the result of poor preservation. Although the MS pattern still cannot be properly observed, the anterior scar is definitely hook-shaped. The oldest specimen recovered, from the lowest beds exposed at the base of the Umzamba cliff section, has a concavity at the posterior end of the VM, but this may be caused by slight crushing of the specimen. New catalogue numbers have been allocated to the type material following transfer to the South African Museum: holotype MG–1–2–6 = SAM–PC6530; paratype MG–1–2–8 = SAM–PC6531; MG–1–2–7 = SAM–PC6532.

Age and distribution

Veenia obesa is confined to Santonian II to III strata at Umzamba, where it reaches 15 per cent of the total ostracod population at the base of the Santonian III zone. It is absent from the highest ostracod-bearing sample collected in Santonian III.

Family **Cytherideidae** Sars, 1925

Genus *Krithe* Brady, Crosskey & Robertson, 1874

This genus, which is indicative of relatively deep-water environments, is relatively abundant in the Campanian IV–Maastrichtian II of Zululand, and has been recorded in the Maastrichtian of the J(c)–1 borehole. The present study records the earliest appearance of the genus in southern Africa (Upper Cenomanian).

Krithe sp. 2329

Fig. 22A–B

Remarks

No internal views were available for this species (2 carapaces), but it differs from *K. nibelaensis*, which is the important Campanian–Maastrichtian Zululand species, by its larger overall size, and lower length/height ratio: *Krithe* sp. 2329 = 1,74; *K. nibelaensis* = 2,07.

Age and distribution

Uppermost Cenomanian (2 201 m, 7 720 ft) to Turonian (2 152 m, 7 076 ft), J(c)–1 borehole.

Krithe sp. 2332

Fig. 22C

Remarks

One crushed carapace of an elongate species. Its valve outline serves to distinguish it from *Krithe* sp. 2329 and *K. nibelaensis*, but its relationship to *Krithe* sp. A from the Maastrichtian of the J(c)–1 borehole (Dingle 1981), which is also relatively elongate, is not known.

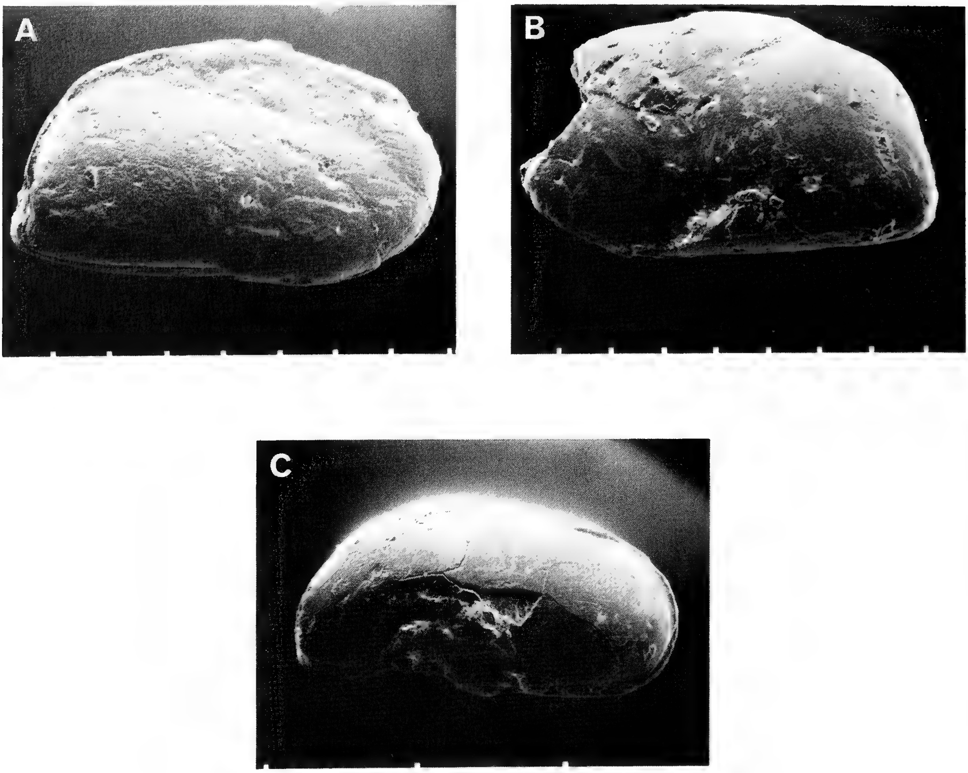


Fig. 22. *Krithe*, J(c)–1 borehole. A. *Krithe* sp. 2329, SAM–PC6536, RV, 2 152 m, Turonian, SEM 2330. B. *Krithe* sp. 2329, SAM–PC6537, LV, 2 201 m, Upper Cenomanian, SEM 2333. C. *Krithe* sp. 2332, SAM–PC6538, RV, 2 176 m, Turonian, SEM 2331. Scale bars: A–B = 100 μ, C = 300 μ.

Age and distribution

Turonian, 2 176 m (7 140 ft), J(c)–1 borehole.

Family **Trachyleberididae** Sylvester-Bradley, 1948

Subfamily Unicapellinae Dingle, 1981

Seven genera have been recognized in this subfamily, which was at its most diverse in the late Cretaceous. All range into the Maastrichtian, and five occur in Campanian strata (Fig. 23). *Unicapella* is the first to appear (Coniacian), but *Herrigocythere, Dutoitella, Paleoabyssocythere*, and *Atlanticythere* all have their first records more or less simultaneously (Campanian) in widely scattered locations (?California, southern Africa, south Atlantic). Benson's (1977) and Dingle's (1981) work suggests that the Southern Hemisphere genera had adapted to relatively deep-water environments during the Cretaceous, and that some persisted into the Tertiary as typical deep-water, cosmopolitan taxa. Similar

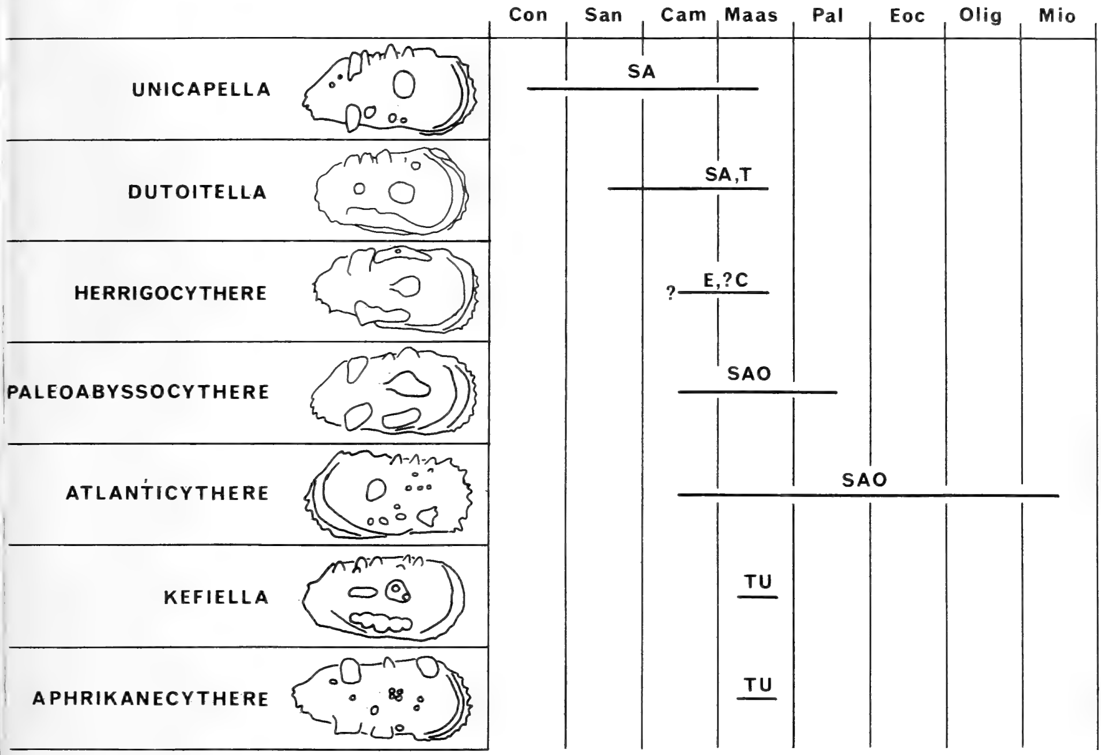


Fig. 23. Ranges of genera of the subfamily Unicapellinae. Key to localities: SA = south-east Africa, T = Tanzania, E = Europe, C = California, SAO = South Atlantic Ocean, TU = Tunisia. References cited in the text.

conclusions were reached by Donze *et al.* (1982) on the Tunisian forms, where *Kefiella* and *Aphrikanecythere* inhabited oxygen-depleted waters (4–5 ml/ℓ) at 400–500 m depths on the upper continental slope.

Genus *Unicapella* Dingle, 1980

Three species of this genus are known from southern Africa, only one of which occurs in Coniacian–Santonian strata (Table 7): *U. stragulata* (Coniacian–Santonian); *U. sacsi* (Campanian–Maastrichtian); and *U. reticulata* (Campanian).

Unicapella stragulata sp. nov.

Fig. 24A–F

Derivation of name

Latin *stragulum* (carpet, rug)—fanciful reference to the carpet-like texture of surface ornamentation.

TABLE 7

Distribution of *Unicapella* and *Dutoitella* in south-east Africa.

	Coniacian	Santonian	Campanian	Maastrichtian	
Unicapella					
stragulata					
reticulata					
sacsi					
Dutoitella					
mimica					
dutoiti					

Holotype

SAM–PC6539, RV, locality 15–7, Mtubatuba, Coniacian IV.

Paratypes

SAM–PC6540, RV, locality 74–13, False Bay, Santonian III.
SAM–PC6541, LV, locality 74–9, False Bay, Santonian ?II.

Diagnosis

Species with short, elliptical ventrolateral ridge, ornamented overall with coarse primary, and fine secondary reticulation.

Description

External features. Elongate nodose appearance. AM broadly rounded with numerous coarse spines, PM bluntly acuminate, asymmetrically so in LV. DM straight, but obscured by lateral surface elevations, VM straight, but obscured about mid-length by slight ventral overhang of lateral surface, and in RV there is a distinct concavity in the anteroventral position. There is a prominent, broad anterior hinge ear in LV. Surface ornamentation dominated by smooth, dome-like SCT. Large complex bullae occur in posteroventral and posterodorsal positions. DM has a line of four high, rounded, perforate tubercles, and VM has a wide, short, rounded and curved ventrolateral ridge that incorporates three indistinct tubercles. Further tubercles occur in posterior and median areas. There is a small indented lip on the anteroventral end of the nodous AM rim. Intercostal and internodose areas ornamented with a coarse but indistinct network of narrow ribs, forming a primary reticulation. There is a secondary fine reticulation that imparts a textured appearance that fancifully resembles a carpet. Large and small punctate nodes act as foci for the primary reticulation.

Internal features. No satisfactory interior views.

Remarks

Unicapella stragulata is very close to *U. sacsi*, and differentiation is based on subtle differences in disposition of surface nodes and primary reticulation patterns in the anterior area. These can be summarized (Fig. 25):

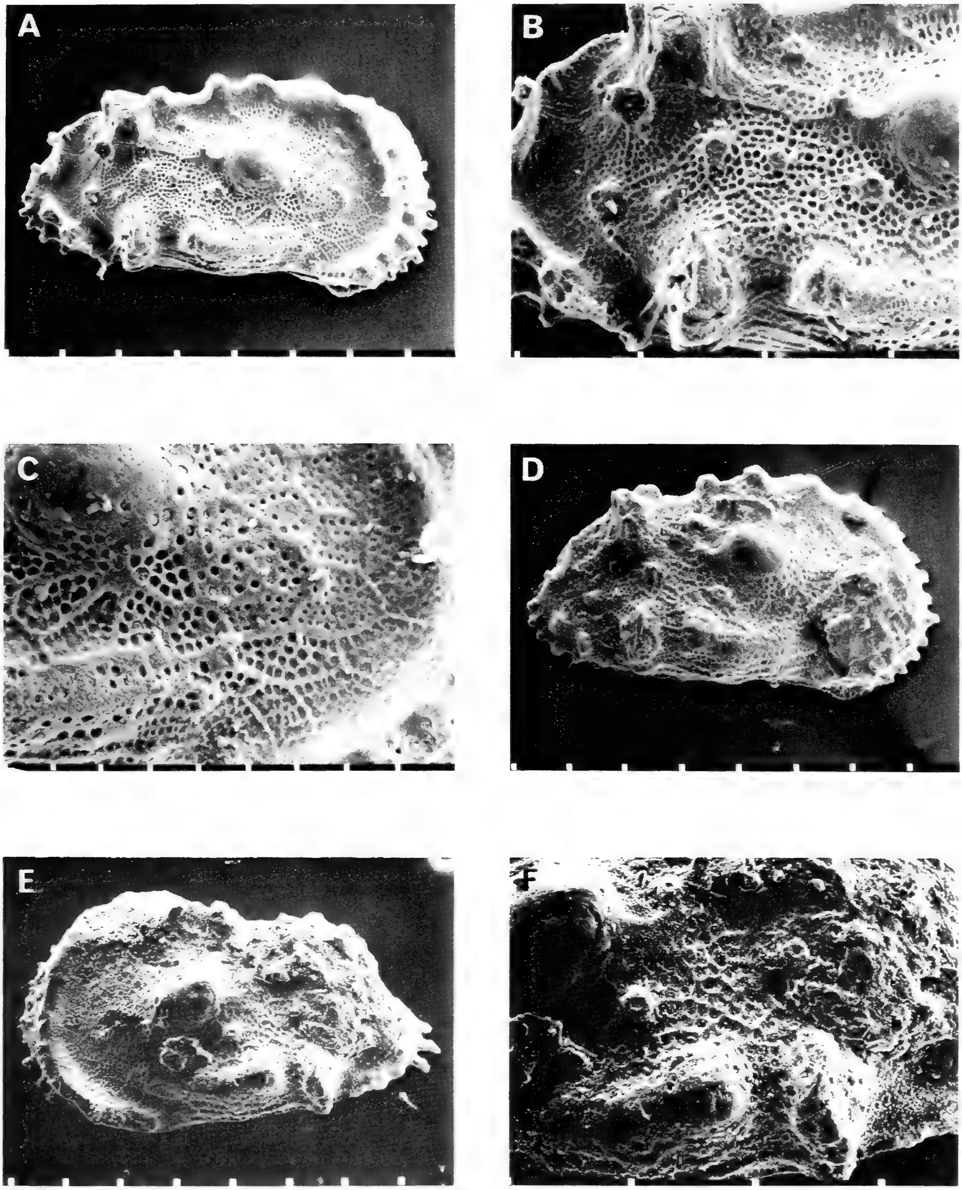


Fig. 24. *Unicapella stragulata* sp. nov. A–C. SAM–PC6539, holotype, RV, locality 15–7, Mtubatuba, Coniacian IV. A. SEM 1948. B. Detail of posterior area, SEM 1951. C. Detail of anterior area, SEM 1950. D. SAM–PC6540, RV, locality 74–13, False Bay, Santonian III, SEM 1868. E–F. SAM–PC6541, LV, locality 74–9, False Bay, Santonian II. E. SEM 1789. F. Detail of area posterior to SCT, SEM 1791. Scale bars: A–B, D–F = 100 μ, C = 30 μ.

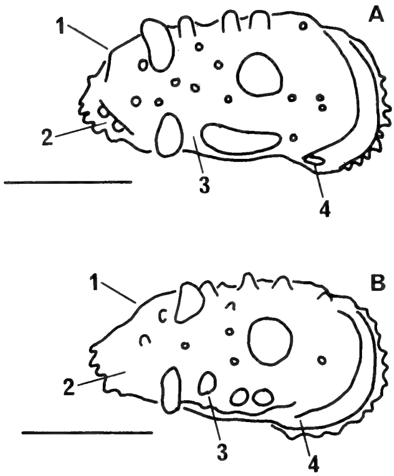


Fig. 25. Comparison of outline of holotypes of *Unicapella*. Significant differences are arrowed. A. *U. stragulata* sp. nov., SAM–PC6539, RV, locality 15–7, Mtubatuba, Coniacian IV, SEM 1948. B. *U. sacsi* SAM–K5610, BH9 Richards Bay, 88,39 m, Campanian II, SEM 343.
Scale bars = 300 μ.

(i) Ventrolateral area: in *U. stragulata* the ornamentation consists of a large bulla and a smooth ridge, whereas in *U. sacsi* there is an additional large node between the bulla and ridge.
(ii) Posterodorsal area: in *U. stragulata* there is a short angled rib in the RV, which is lacking in *U. sacsi*, whereas in *U. sacsi* in both valves there are two small prominent punctate nodes immediately posterior of the posterodorsal bulla.
(iii) Ornamentation of the anterior area: in *U. sacsi* there is a broad band of noticeably fine foveolate ornamentation bounded by the AM rim and a narrow primary rib line. This band is lacking in *U. stragulata*, which has a subtly different primary reticulation pattern, but no noticeable fining in the anteriormost secondary reticulation.

The closeness of the two species strongly suggests that *U. sacsi* developed directly from *U. stragulata* by a slight reorganization of its ornamentation during late Santonian–early Campanian time.

Dimensions (mm)

	length	height
PC6539	0,71	0,36
PC6540	0,70	0,38
PC6541	0,74	0,41

Age and distribution

Unicapella stragulata is known to range Coniacian IV (Mtubatuba) to Santonian III (False Bay) in Zululand.

Genus *Dutoitella* Dingle, 1981

Dutoitella mimica Dingle, 1981

Fig. 26A–B

Genus C sp. Bate, 1969, in Bate & Bayliss: 143, pl. 7 (fig. 15).
Trachyleberis schizospinosa Dingle, 1971*b*: 406–408, fig. 10 (*partim*).
Dutoitella mimica Dingle, 1981: 88–91, figs 37F, 41A–F, 42A–B, 43B, 44B.

Remarks

One worn carapace has been recovered from the J(c)–1 borehole below the levels recorded by Dingle (1981). There is no significant morphological difference between the J(c)–1 specimens and those from the Agulhas Bank. The levels at which this species occur in J(c)–1 are thought to represent intermediate water depths (?100–200 m).

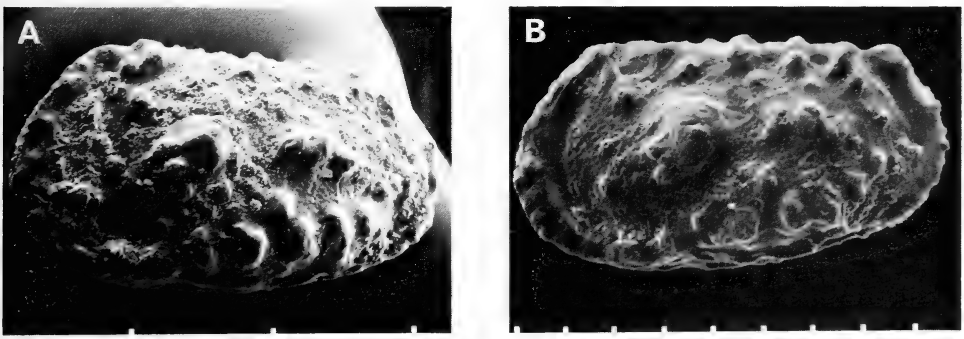


Fig. 26. *Dutoitella mimica*, J(c)–1 borehole. A. SAM–PC6543, LV, 2 030 m, Santonian, SEM 2316. B. SAM–K5752, LV, 1 811 m, Maastrichtian, SEM 1287. Scale bars: A = 300 μ, B = 100 μ.

Age and distribution

Santonian–Maastrichtian, J(c)–1 borehole: levels 2 030 m (Santonian), 1 871 m (Campanian), 1 811 m (Maastrichtian); Maastrichtian III (sample TBD 818, Agulhas Bank), and Maastrichtian (Tanzania, as Genus C sp. Bate, 1969).

Subfamily Trachyleberidinae Sylvester-Bradley, 1948

Genus *Cythereis* Jones, 1849

Altogether five species of this genus have been recorded from east and south-east Africa in Turonian to Maastrichtian strata (Table 8).

TABLE 8

Distribution of *Cythereis* in south-east Africa.

Locality	Species	Coniacian					Santonian			Campanian			
		I	II	III	IV	V	I	II	III	I	II	III	
Umzamba	*transkeiensis*												
BH9	*transkeiensis*												
	klingeri												
Zululand	*transkeiensis*												
	klingeri												
	mfoloziensis												
	cf. *luzangaziensis*												

Cythereis klingeri Dingle, 1980

Figs 27A–F, 28A–B, 30C–D, 31A–E

Cythereis klingeri Dingle, 1980: 34–38, figs 18B–F, 19A–F; 1981: 108–109, fig. 52A.

Remarks

Dingle (1980) noted that there is considerable intraspecific morphological variation in this species in samples from the Richards Bay BH9 borehole (Santonian II to Campanian II). In general terms this gives rise to two main morphotypes: FP (with flared dorsal ridges and pointed PM, especially in LV), and SQ (with subdued dorsal ridges and a more quadrate PM in LV). The holotype of the species belongs to the FP morphotype, and although this variety is more abundant in the Campanian and younger sediments, both types do occur in the oldest sediments in the Richards Bay BH9 borehole (Santonian II). The oldest record of *C. klingeri* is in the Coniacian IV, where the species is relatively abundant. Here the specimens are morphologically intermediate between the main FP and SQ morphs, but tend to have more characters typical of the former. This distribution leads to two conclusions: firstly that the two morphs are not sexual dimorphs, and secondly that the FP morph, although more abundant in the younger strata in BH9, was not a later development.

Cythereis klingeri is closely related to *C. luzangaziensis* from the Upper Turonian of Tanzania (Bate & Bayliss 1969) (Figs 28D, 31G–H), but differs principally in the shape of the ventrolateral ridge. In *C. luzangaziensis*, this ridge loops round at its posterior termination to form a narrow but prominent rib on the ventral surface that runs anteriorly, but is not contiguous with the AM rim. This ventral surface rib does not occur in *C. klingeri*. A phylogenetic relationship between the two species seems very probable, with speciation into *C. klingeri* taking place in Coniacian I–III time.

Age and distribution

Cythereis klingeri occurs in Santonian II to Campanian III strata in BH9 borehole, and in Coniacian IV (locality 15–9 to 15–15, Mtubatuba) and

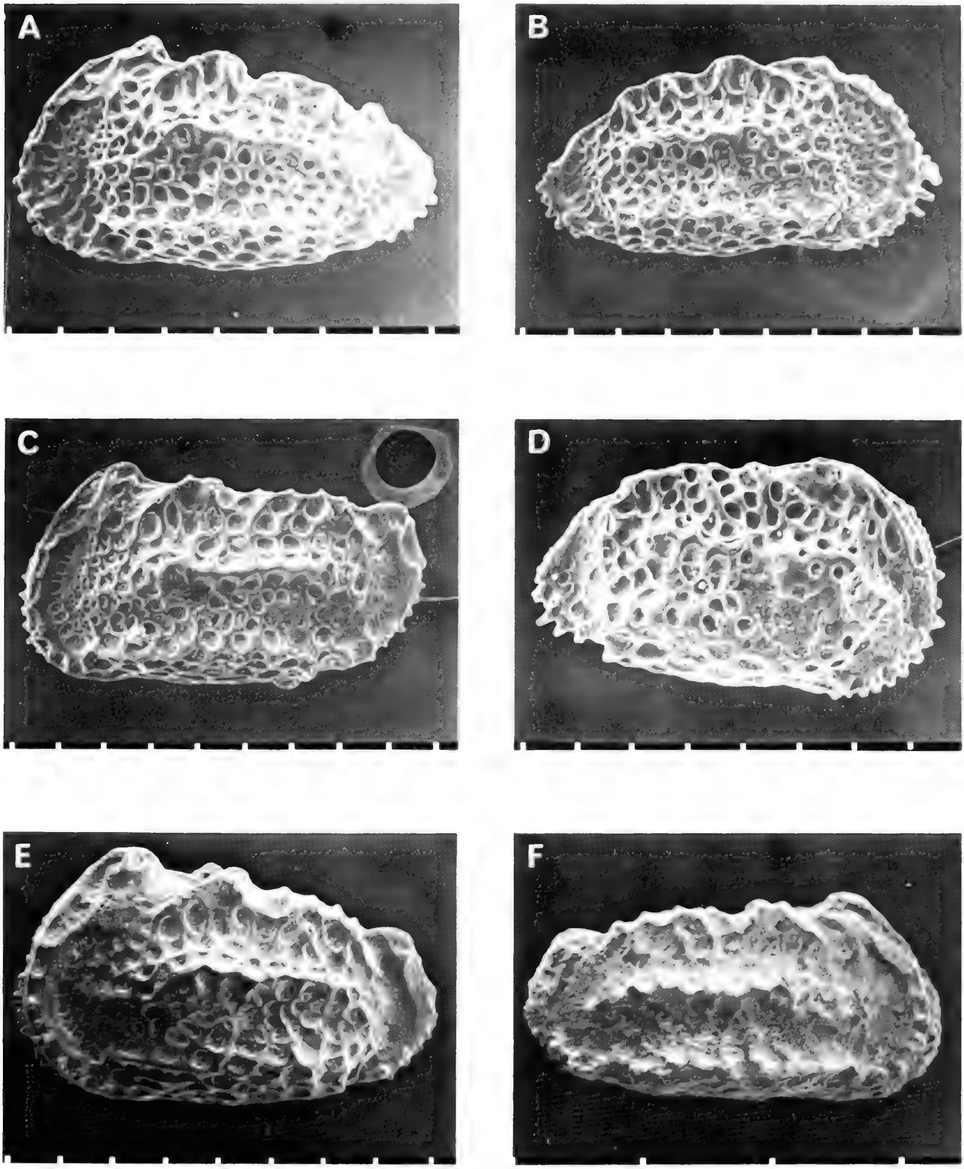


Fig. 27. *Cythereis klingeri*. A. SAM–K5617, LV, BH9 Richards Bay, 82,03 m, Campanian II, FP variety, SEM 158. B. SAM–K5616, holotype, RV, BH9 Richards Bay, 82,03 m, Campanian II, FP variety, SEM 165. C. SAM–K5622, LV, BH9 Richards Bay, 157,0 m, Santonian II, SQ variety, SEM 200. D. SAM–PC6544, RV, BH9 Richards Bay, 151,1 m, Santonian II, SQ variety, SEM 195. E. SAM–PC6545, LV, locality 15–5, Mtubatuba, Coniacian IV, FP variety, SEM 2035. F. SAM–PC6546, RV, locality 15–5, Mtubatuba, Coniacian IV, SQ variety, SEM 2036.
Scale bars: A–E = 100 μ, F = 300 μ.

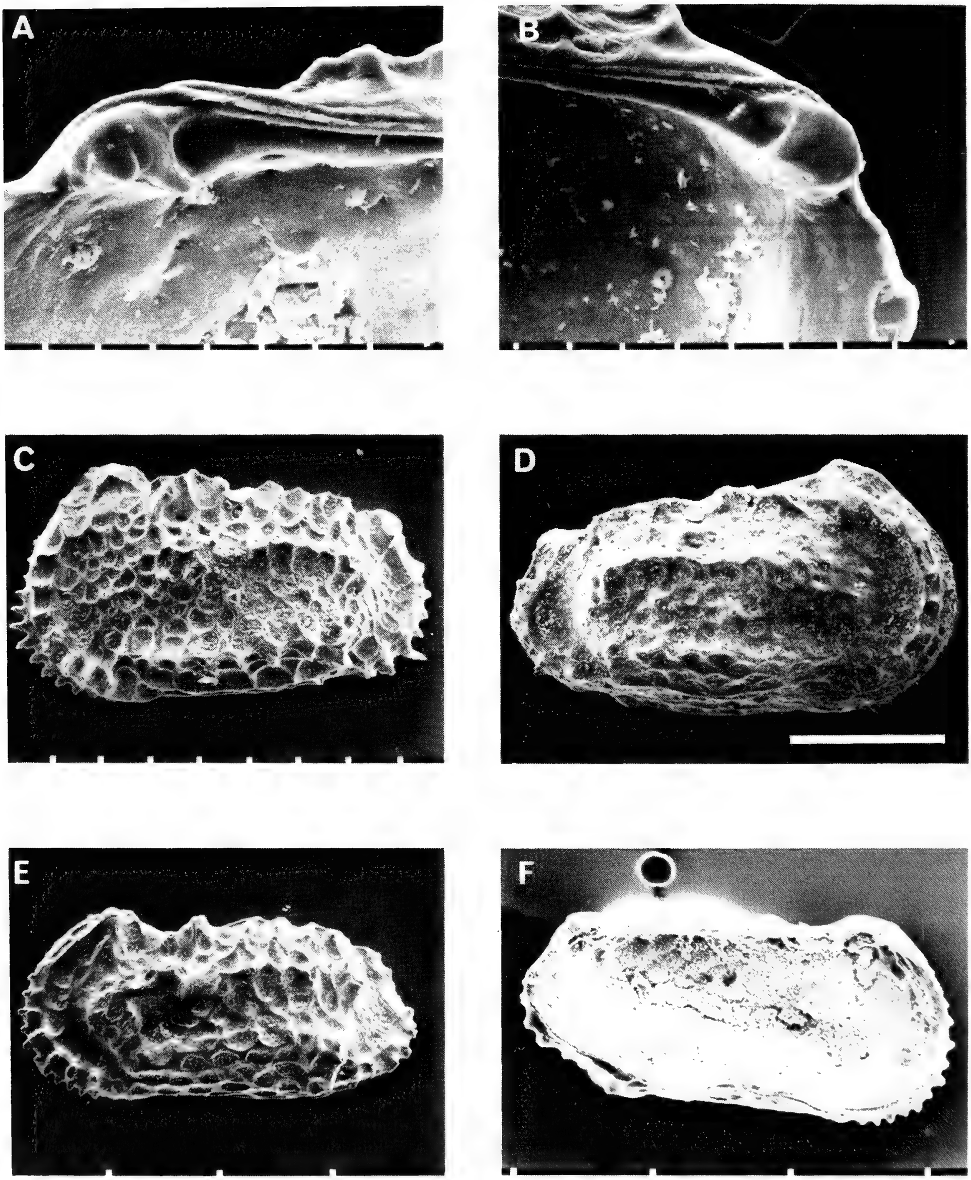


Fig. 28. *Cythereis*. A–B. *C. klingeri*, SAM–K5620, RV, BH9, Richards Bay, 157,0 m, Santonian II. A. ATE, SEM 207. B. PTE, SEM 208. C. *C.* cf. *luzangaziensis*, SAM–PC6547, LV, locality 15–5, Mtubatuba, Coniacian IV, SEM 1936. D. *C. luzangaziensis*, BMNH Io792, holotype, RV, Wami River area, Luzangazi Stream, Tanzania, Turonian, SP7/846. E–F. *C. mfoloziensis* sp. nov., SAM–PC6548, holotype, LV, locality 16–1, Mtubatuba, Coniacian II. E. SEM 1941. F. Internal view, SEM 2159.
Scale bars: A–B = 30 μ, C = 100 μ, D–F = 300 μ.

Campanian II to Maastrichtian II (Mfolozi and Nibela areas) at outcrop in Zululand. It does not occur in Santonian–Campanian strata at Umzamba. Dingle (1981) concluded that it is an environmentally tolerant species, but that it probably preferred relatively shallow (<100 m) water.

Cythereis cf. *luzangaziensis* Bate, 1969

Figs 28C, 31I

Cythereis luzangaziensis Bate, 1969 in Bate & Bayliss: 134, pl. 6 (fig. 10).

Remarks

One specimen showing the characteristic ventrolateral ridge loop has been found in the present study. It differs from the Tanzanian material by having a marked depression (almost a break) between the median longitudinal ridge and the SCT. There is a relatively good population of *C. klingeri* in the sample so I am confident that this specimen is not a morphotype of this species, because there are several distinct differences: shape of anteriormost lobe on the DM ridge, shape of SCT, ventrolateral rib pattern, markedly coarser reticulate ornament and strongly elevated muri and ridges in *C.* cf. *luzangaziensis*. Figures 28D and 31G–H show type specimens of *C. luzangaziensis* for comparison.

Age and distribution

Known only from Coniacian IV (locality 15–13, Mtubatuba) in Zululand.

Cythereis mfoloziensis sp. nov.

Figs 28E–F, 31F

Derivation of name

Locality of type—Mfolozi River valley, Zululand.

Holotype

SAM–PC6548, LV, locality 16–1, Mtubatuba area, Coniacian III.

Diagnosis

Species of *Cythereis* with a complex tubercle lying in an anteroventral position relative to the SCT.

Description

External features. Elongate subquadrate in outline. AM symmetrically rounded, PM triangular with apex just below mid-height. DM and VM straight. Lateral surface carries three prominent longitudinal ridges. Dorsal ridge obscures DM and is flared with a prominent peak at its anterior end. Median ridge is short, descends slightly anteriorly, terminates at about mid-length and is linked to the dorsal ridge by a low saddle. Ventral ridge is straight, terminates posteriorly in a

right-angled bend towards the VM and anteriorly hooks upward to join the complex tubercle. SCT is prominent, rounded and is linked by a short rib to the complex tubercle that lies anteroventrally to it. The latter is formed by a knot of reticulating muri. There is a strong spinose AM rim. Surface overall is coarsely reticulate. The eye tubercle is almost turreted at the prominent ACA.

Internal views. Internal features are poorly preserved. MS not seen, and MA broken. ATE in LV has a prominent process at its anterior end, which indicates a closer relationship to *C. klingeri* than to *C. transkeiensis*, although overall the ATE of *C. mfoloziensis* is less massive than in *C. klingeri*.

Remarks

Cythereis mfoloziensis is closest to *C. klingeri*, from which it differs on the following points: its median ridge does not connect to the SCT, it possesses a tubercle adjacent to the SCT, and has a more prominent posterior termination to the ventrolateral ridge. The distinctive morphology of *C. mfoloziensis* justifies the erection of the species on one specimen only.

Dimensions (mm)

	length	height
PC6548	1,05	0,51

Age and distribution

Known only from the Coniacian III (locality 16, Mtubatuba) of Zululand.

Cythereis transkeiensis Dingle, 1969

Figs 29A–F, 30A–B

?Cythereis ornatissima Reuss, 1846, var. *reticulata* [*non*] Jones & Hinde, 1890, Chapman 1904: 234.

Cythereis transkeiensis Dingle, 1969: 377–378, fig. 18; 1980: 34, fig. 18A; 1981: 109, fig. 52B–C.

Remarks

Closely allied to *C. klingeri, C. transkeiensis* can be distinguished by its massive lateral longitudinal ridges and hinge structure. The holotype is illustrated here (Fig. 30), showing that the hinges of the two species differ as follows: ATE RV in *C. klingeri* resembles a right-hand fist, with external 'thumb', and in *C. transkeiensis* is a left-hand fist; anterior part of ME RV is an enclosed hollow in *C. transkeiensis*, but has no posterior wall in *C. klingeri*; ATE LV in *C. klingeri* has a posterior projection on the anterior wall, while this is lacking in *C. transkeiensis*. Bate's *Cythereis* sp. C (*in* Bate & Bayliss 1969, pl. 7 (fig. 4)) is similar in outline and ornamentation to *C. transkeiensis*.

Age and distribution

Cythereis transkeiensis ranges Santonian II to Campanian I at Umzamba. It is known from Santonian II in Richards Bay BH9 borehole, Santonian III at outcrop in Zululand (locality 14, Msunduzi River), and late Campanian–early

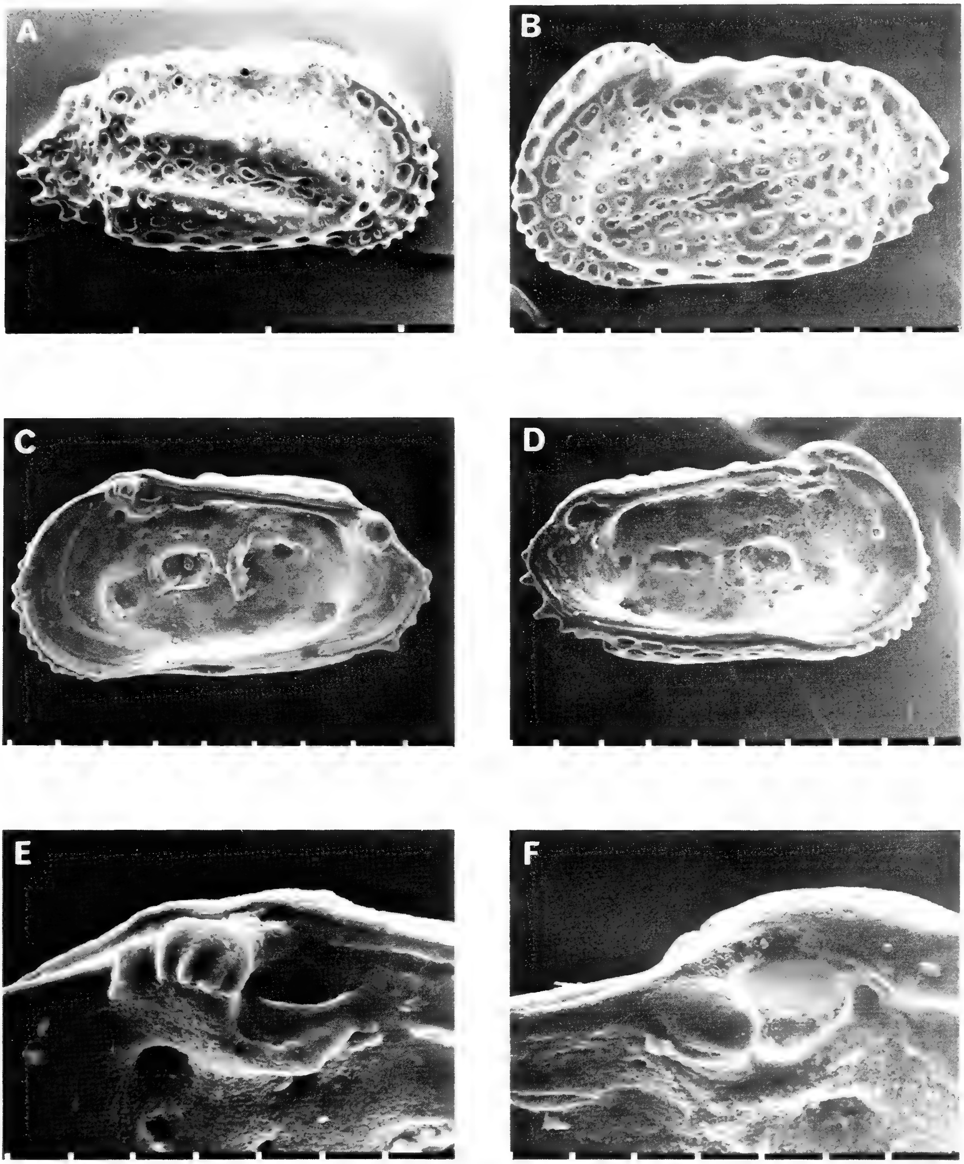


Fig. 29. *Cythereis transkeiensis*, Umzamba. A. SAM–PC6549, holotype, RV, bed 1, Santonian II, SEM 2121. B. SAM–PC6550, LV, bed 3, Santonian III, SEM 145. C. SAM–PC6551, RV, internal view, bed 3, Santonian III, SEM 147. D. SAM–PC6552, LV, internal view, bed 3, Santonian III, SEM 152. E. SAM–PC6551, RV, ATE, bed 3, Santonian III, SEM 149. F. SAM–PC6552, LV, ATE, bed 3, Santonian III, SEM 154.
Scale bars: A = 300 μ, B–D = 100 μ, E–F = 30 μ.

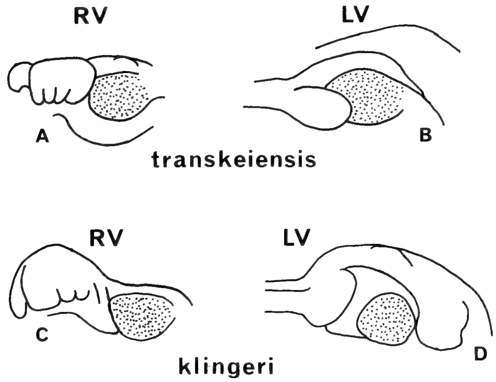


Fig. 30. Comparison of anterior terminal hinge elements of *Cythereis transkeiensis* and *C. klingeri*. A. SAM–PC6551, Umzamba bed 3, Santonian III. B. SAM–PC6552, Umzamba bed 3, Santonian III. C. SAM–K5620, BH9 Richards Bay, 157,0 m, Santonian II. D. SAM–K5619, BH9 Richards Bay, 157,0 m, Santonian II.

Maastrichtian at Igoda. This is a total range of Santonian II to late Campanian–early Maastrichtian. *Cythereis transkeiensis* is rare north of Umzamba, and clearly is a southern analogue of *C. klingeri*, which itself is effectively restricted to Zululand.

Genus *Haughtonileberis* Dingle, 1969

Grosdidier (1979) provisionally assigned five species to *Haughtonileberis* from borehole material in Gabon. These are the earliest records of the genus, with '*Haughtonileberis*' GA C11 (Upper Albian–Upper Cenomanian), followed by three Upper Cenomanian appearances.

The earliest representative in south-east Africa is *H. haughtoni* (Coniacian) (also recorded by Bate & Bayliss (1969) from the Upper Turonian of Tanzania), which ranges into the Lower Campanian. Two other species (*H. fissilis* and *H. vanhoepeni*) are known from the Santonian of south-east Africa.

These records suggest a generic range of Upper Albian to Lower Oligocene (Table 9), with the initial development of the genus in the Equatorial Atlantic (i.e. north of the Walvis Ridge), and rapid migration into the south-west Indian Ocean area by Turonian–Coniacian times.

Haughtonileberis haughtoni Dingle, 1969

Fig. 32A–F

Haughtonileberis haughtoni Dingle, 1969: 372–373, fig. 15; 1980: 39, fig. 21A–E.
Curfsina turonica Bate, 1969, in Bate & Bayliss: 139, pl. 6 (figs 15, 19) (*partim* (BMNH Io783)).

Remarks

Coniacian specimens from south-east Africa are of the squat variety noted by Dingle (1969, 1980) in the topotypic populations, but they possess the sharper,

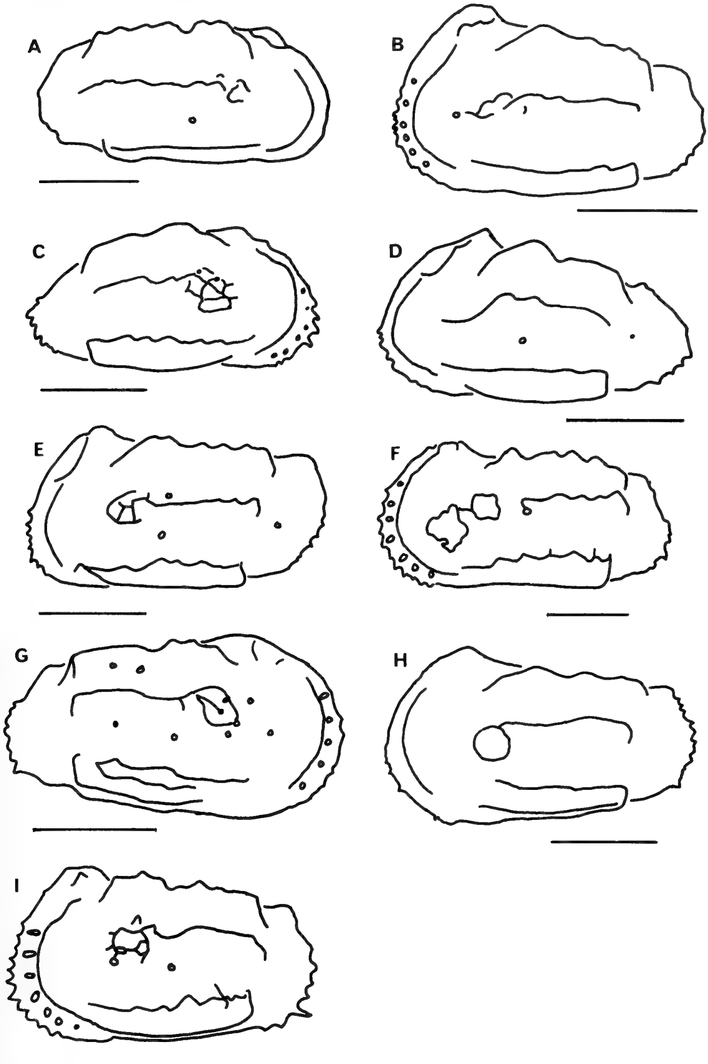


Fig. 31. Comparison of lateral outlines of various species of *Cythereis*. A–E. *C. klingeri*. A. SAM–PC6546, RV, Coniacian IV. B. SAM–PC6545, LV, Coniacian IV. C. SAM–K5616, RV, Campanian II. D. SAM–K5617, LV, Campanian II. E. SAM–K5622, Santonian II. F. *C. mfoloziensis* sp. nov., SAM–PC6548, Coniacian III. G–H. *C. luzangaziensis*, BMNH Io792, holotype, carapace, Turonian. G. RV. H. LV. I. *C.* cf. *luzangaziensis*, SAM–PC6547, LV, Coniacian IV. Scale bars = 300 μ.

TABLE 9

Distribution of *Haughtonileberis* in Africa and adjacent areas.

	Alb.	Cen.	Tur.	Con.	Sant.	Camp.	Maas.	Pal.	Eoc.	Olig.
GABON										
GA C11†										
triangulata†										
GA A30†										
GA F15†										
GA D8†										
TANZANIA										
haughtonileberis§										
SOUTH AFRICA										
haughtonileberis‘										
fissilis‘										
vanhoepeni‘										
nibelaensis‘										
radiatus“										
TUNISIA										
*acies**										
IRAN										
?*Dumontina* IR E18$										

† = Grosdidier (1979)
§ = Bate & Bayliss (1969) one paratype of *Curfsina turonica* (BMNH Io783)
‘ = Dingle (1981)
“ = Dingle (1976)
* = Donze *et al.* (1982)
$ = Grosdidier (1973), similar morphology

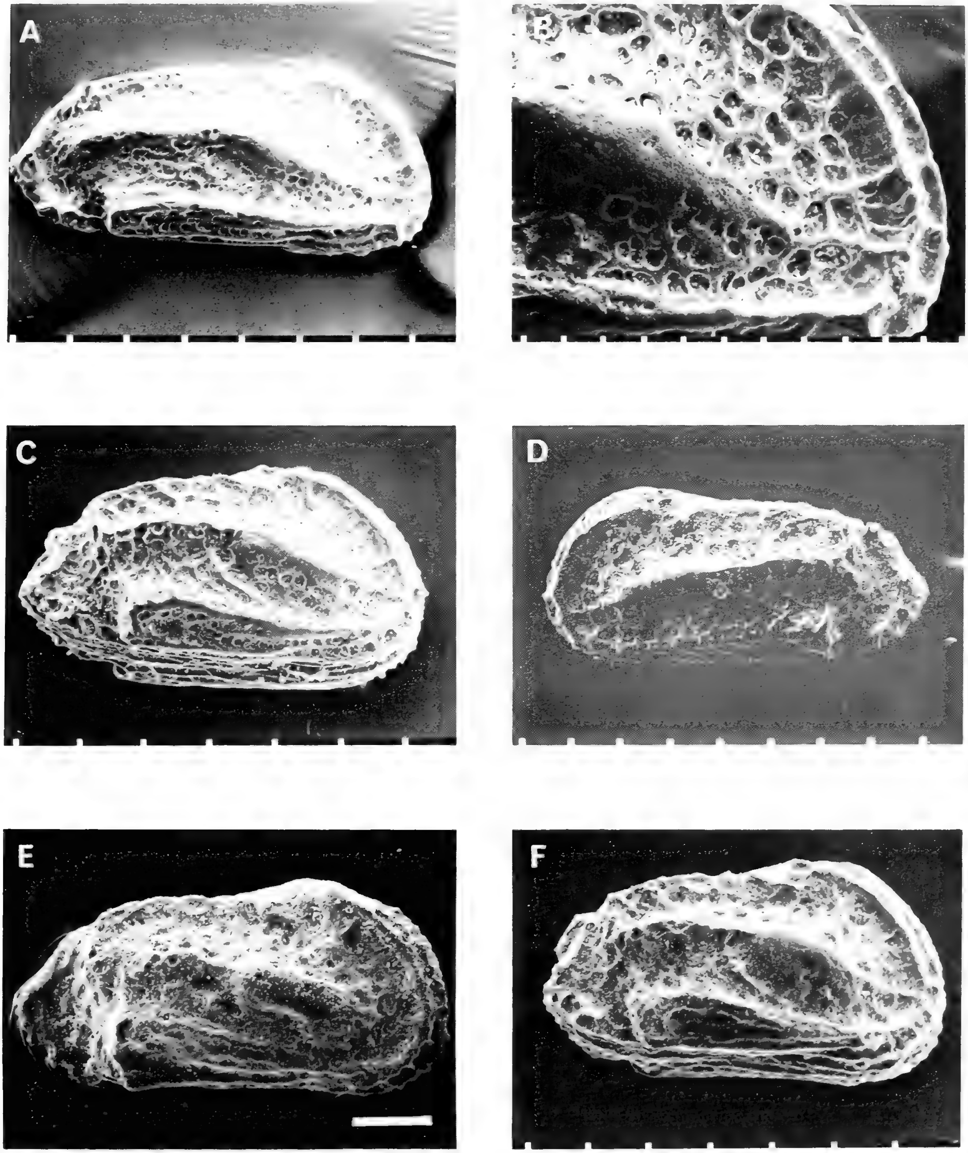


Fig. 32. *Haughtonileberis haughtoni*. A–B. SAM–PC6553, holotype, RV, Umzamba bed 1, Santonian II. A. SEM 2117. B. Detail of anterior area, SEM 2119. C. SAM–PC6554, RV, locality 15–5, Mtubatuba, Coniacian IV, SEM 1945. D. SAM–PC6556, LV, locality 14–3, Mtubatuba, Santonian III, SEM 1780. E. BMNH Io783, RV, described by Bate (*in* Bate & Bayliss 1969) as paratype of *Curfsina turonica*, Wami River area, Luzangazi Stream, Tanzania, Turonian, SP7/854. F. SAM–PC6555, RV, locality 89, Hluhluwe River, Coniacian IV, SEM 1943. Scale bars: A, D–F = 100 μ, B = 30 μ.

narrow posteromedian ridge of the Zululand Campanian faunas. Bate (*in* Bate & Bayliss 1969) illustrated a specimen, which I consider is *H. haughtoni*, as a paratype for his new species *Curfsina turonica* from the Upper Turonian of Tanzania. The holotype (pl. 6 (figs 13, 18, BMNH Io784)) differs significantly from BMNH Io783 in the following points: shape of the ventrolateral ridge, shape of median lateral ridge and SCT, shape of PCA, and shape of PM outline.

Of the five species tentatively assigned to *Haughtonileberis* by Grosdidier (1979) from Gabon, *Haughtonileberis?* GA F15 (Upper Cenomanian–Lower Turonian) is closest to the type species. The main difference is a more prominent upswing in the posterior part of the ventrolateral rib. Otherwise, the general outline, ornamentation, and in particular the shape of the median ridge and adjoined elongate SCT are very similar. The holotype, originally designated MG–1–1–12, has been transferred to the South African Museum under the number SAM–PC6553.

Age and distribution

Upper Turonian of the Luzangazi stream, north of the Wami River, Tanzania; Coniacian IV (locality 15, Mtubatuba) to Campanian I (locality 74, False Bay) at outcrop in Zululand; Santonian II to Campanian I in the Richards Bay BH9 borehole; and Santonian II to Campanian I at Umzamba cliff. This is the longest-ranging species of the genus so far recognized: Upper Turonian to Campanian I. Dingle (1981) concluded that the species was environmentally tolerant (<100 m to 200 m water depths) but that it preferred shallow-water (<100 m), low-energy environments with restricted access to the open ocean.

Haughtonileberis fissilis Dingle, 1969

Fig. 33A–D

Haughtonileberis fissilis Dingle, 1969: 374–375, fig. 16; 1980: 39, fig. 22A–B; 1981: 95, fig. 48F.

Remarks

This species is rare in outcrops in Zululand, where the Santonian specimens belong to the squatter morphotype recognized by Dingle (1980). No significant morphological differences are noted in specimens at the extremes of the species's temporal range. Of the species assigned to *Haughtonileberis* by Grosdidier (1979), '*Haughtonileberis*' GA A30 is closest to *H. fissilis*, having a distinctly split anterior end to the median lateral rib. It differs in having a short oblique dorsal ridge that runs anteriorly from the PCA position. Type material of *H. fissilis* has been transferred to the South African Museum and the new numbers are: MG–1–1–16 = SAM–PC6557, MG–1–1–17 = SAM–PC6559, and MG–1–1–18 = SAM–PC6558.

Age and distribution

Haughtonileberis fissilis ranges Santonian III (Msunduzi River) to Maastrichtian I (Mfolozi River) at outcrops in Zululand, Santonian II to Campanian II in

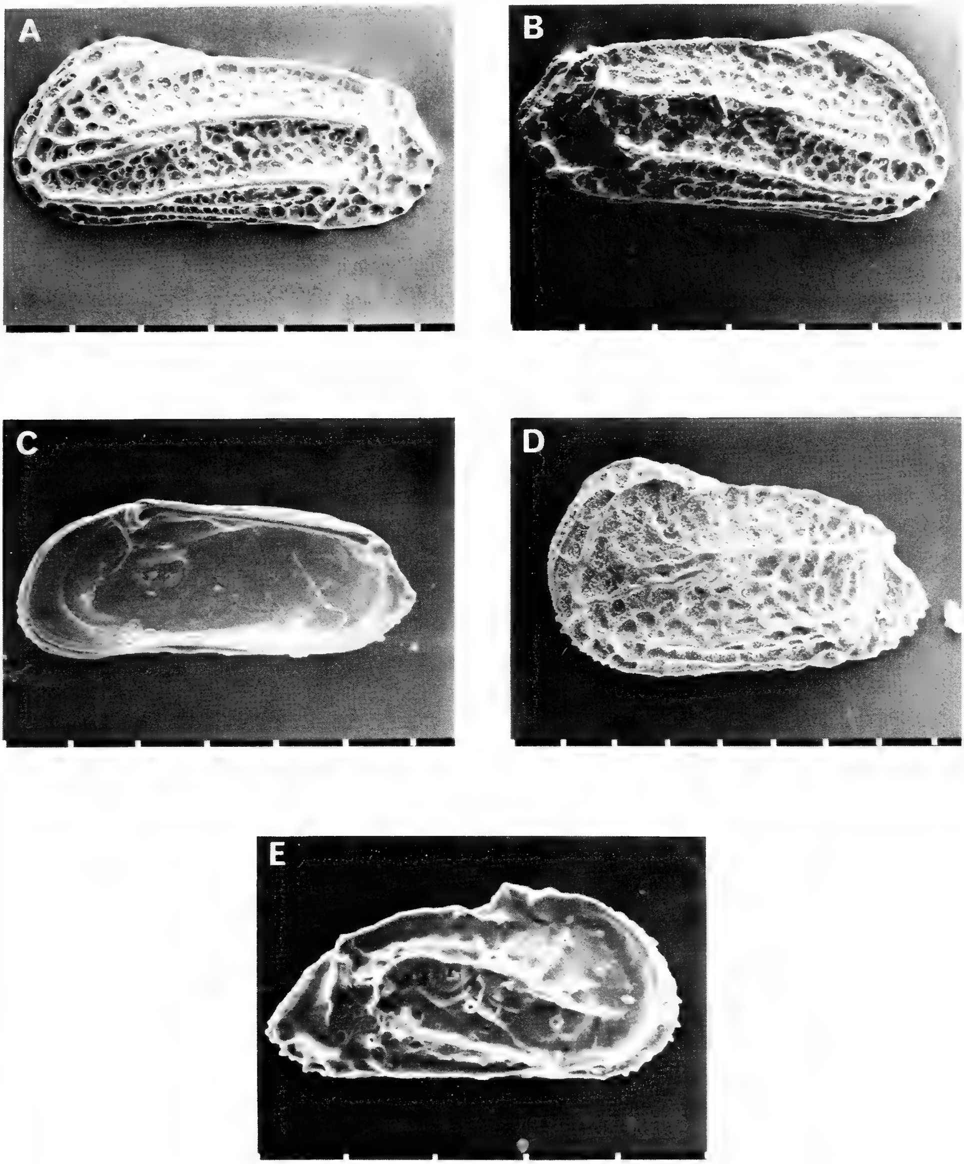


Fig. 33. A–D. *Haughtonileberis fissilis*. A–C. Umzamba bed 1, Santonian II. A. SAM–PC6557, holotype, LV, SEM 2126. B. SAM–PC6558, RV, SEM 2129. C. SAM–PC6559, internal, RV, SEM 254. D. SAM–PC6560, LV, locality 14–1, Mtubatuba, ?Santonian III, SEM 1866. F. *Haughtonileberis vanhoepeni*, SAM–K5632, holotype, RV, BH9, Richards Bay, Campanian I, SEM 32. Scale bars = 100 μ.

the Richards Bay BH9 borehole, and Santonian II to Campanian I at Umzamba. Its total time range in Zululand is Santonian II to Maastrichtian I.

Haughtonileberis vanhoepeni Dingle, 1980

Fig. 33E

Haughtonileberis vanhoepeni Dingle, 1980: 42–44, figs 22H, 23A–F; 1981: 95, fig. 46A.

Remarks

No additional specimens of this species were recovered from Coniacian and Santonian outcrops in Zululand during the present study. None of the species assigned to *Haughtonileberis* by Grosdidier (1979) are close to *H. vanhoepeni.*

Age and distribution

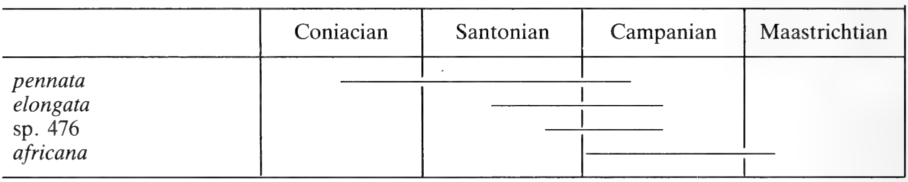
Known only from the Santonian III to Campanian II of the Richards Bay BH9 borehole, and Campanian II to Campanian IV outcrops in Zululand. This gives a total range of Santonian III to Campanian IV, but the Santonian record is restricted to one sample at the very top of Santonian III in BH9. The appearance of *H. vanhoepeni* therefore can be taken as an effective marker for the Santonian–Campanian boundary.

Genus *Oertliella* Pokorny, 1964

This genus first appears in the Coniacian of Zululand, but is relatively rare until the Campanian, where four species are present (Table 10).

TABLE 10

Distribution of *Oertliella* in south-east Africa.



Oertliella pennata Dingle, 1980

Fig. 34A–E

Acanthocythereis? aff. *A. horridula* (Bosquet, 1854), Dingle, 1969: 378–380, fig. 19.
Oertliella pennata Dingle, 1980: 46–49, fig. 26A–E; 1981: 98, fig. 48A.

Remarks

With the exception of the Coniacian specimens from locality 15–5, which have more massive spines, those from horizons at outcrop in Zululand are identical to the topotypes from the Richards Bay BH9 borehole.

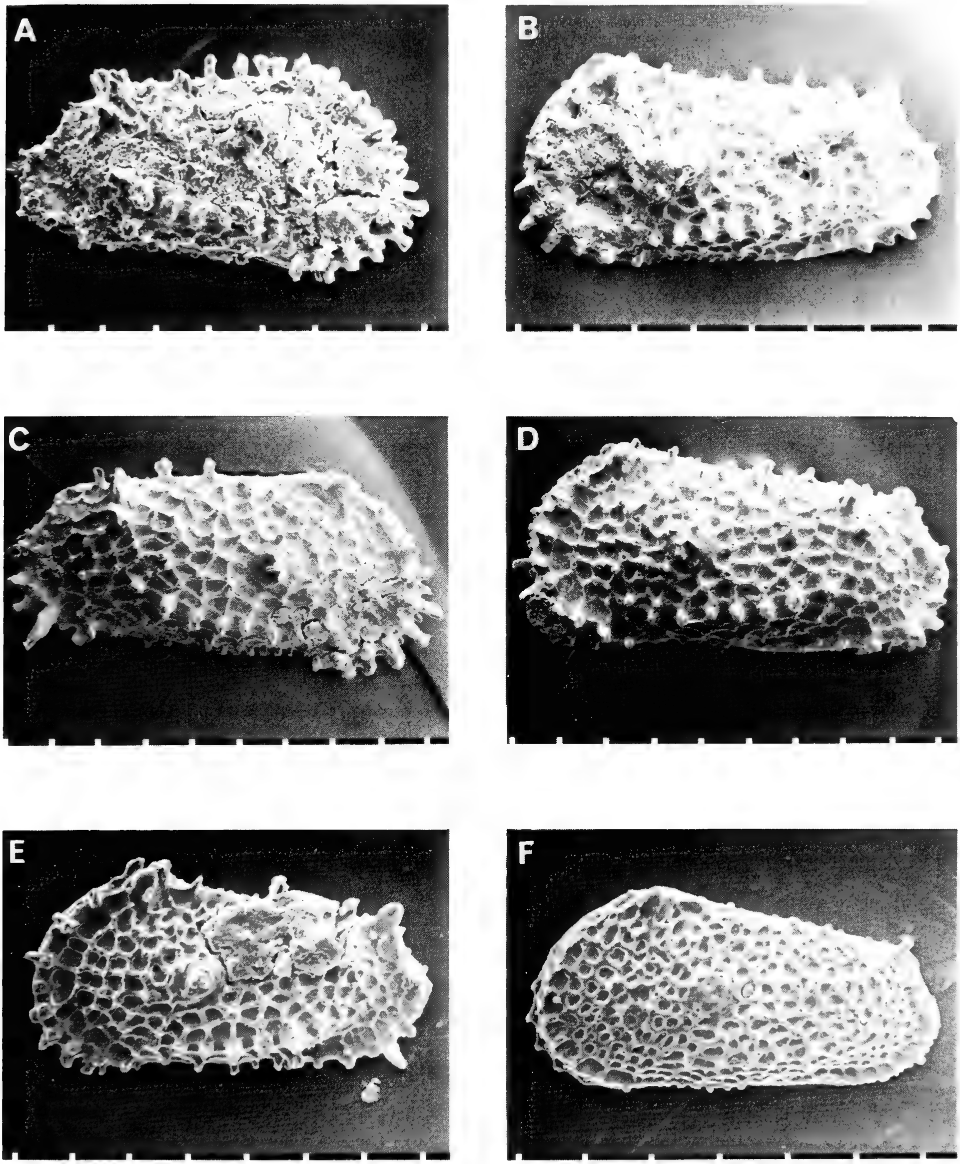


Fig. 34. *Oertliella*. A–E. *O. pennata*. A. SAM–PC6561, RV, locality 15–5, Mtubatuba, Coniacian IV, SEM 1928. B. SAM–PC6562, LV, locality 15–7, Mtubatuba, Coniacian IV, SEM 2135. C. SAM–PC6563, RV, Umzamba bed 7, Santonian III, SEM 2079. D. SAM–PC6564, LV, Umzamba bed 3, Santonian III, SEM 2111. (This is the specimen recorded as *?Acanthocythereis* aff. *A. horridula* by Dingle (1969) (MG–1–2–9)). E. SAM–K5644, holotype, LV, BH9 Richards Bay, 115,9 m, Santonian III, SEM 471. F. *Oertliella* sp. 476, SAM–K5647, LV, BH9 Richards Bay, 115,9 m, Santonian III, SEM 476. Scale bars = 100 μ.

Age and distribution

Coniacian IV to Santonian III (localities 15–5, 15–7, 74–10 and 74–15) at outcrop in Zululand, Santonian III to Campanian II in Richards Bay borehole, and Santonian III to Campanian I at Umzamba.

Oertliella sp. 476

Fig. 34F

Oertliella sp. A Dingle, 1980: 50, fig. 26F.

Remarks

No additional specimens of this species have been recovered during the present study.

Age and distribution

Uppermost Santonian III to Campanian II, Richards Bay BH9 borehole.

Genus *Rayneria* Neale, 1975

Rayneria nealei Dingle, 1980

Fig. 35A–F

Cythereis ?quadrilatera (Roemer) Chapman, 1923: 5, pl. 1 (5).
Rayneria nealei Dingle, 1980: 55–57, figs 28E–F, 29A–F, 30G; 1981: 108, fig. 51F.

Remarks

During the present study several specimens of this species were recorded from Santonian and Coniacian horizons at Umzamba and in Zululand. Compared to type material from the Richards Bay BH9 borehole, which is of Santonian III and Campanian I age, the older populations show several subtle morphological variations. In particular, the valves in lateral outline have a less angular appearance, with the ventromedian ridge being more subdued, while ornamentation in the anterior part of the valve has a distinctly foveolate aspect compared to the more coarsely reticulate ornamentation of the type material. However, one characteristic feature of ornamentation, which both populations display well, is the possession of fine secondary muri within many large individual fossae, which resemble spiders' webs.

Age and distribution

Known from Coniacian IV (Mtubatuba) outcrops in Zululand, Santonian II to lowermost Campanian I in the Richards Bay BH9 borehole, and Santonian III at Umzamba. This gives a total range of Coniacian IV to Campanian I in

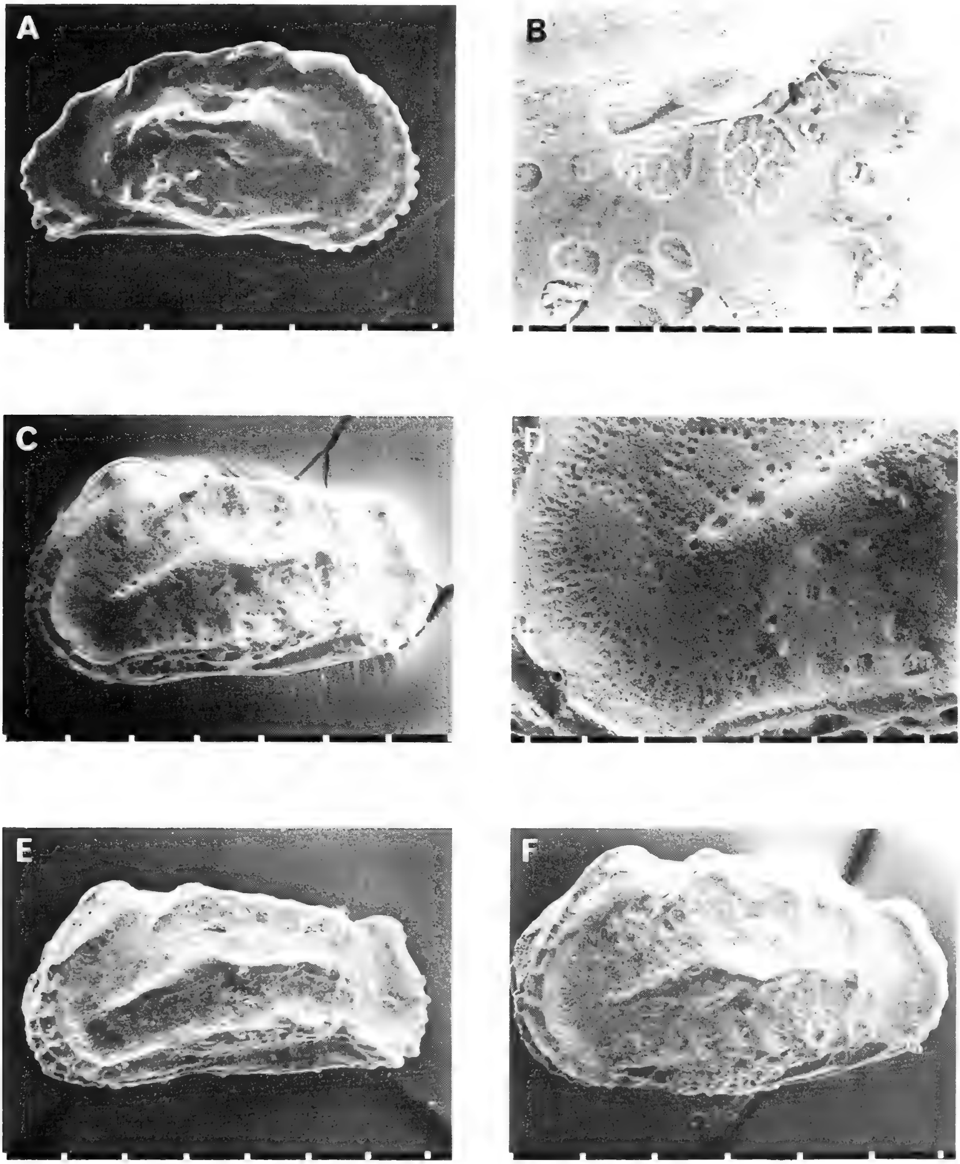


Fig. 35. *Rayneria nealei*. A. SAM–K5652, holotype, RV, BH9, Richards Bay, 139,8 m, Santonian III, SEM 413. B. SAM–PC6567, LV, detail central area, lateral view, Umzamba bed 7, Santonian III, SEM 2083. C–D. SAM–PC6565, LV, Umzamba bed 5, Santonian III. C. SEM 2063. D. Detail anterior area, SEM 2064. E. SAM–PC6566, LV, locality 15–5, Mtubatuba, Coniacian IV, SEM 2042. F. SAM–PC6567, LV, Umzamba bed 7, Santonian III, SEM 2081. Scale bars: A, C, E–F = 100 μ, B = 10 μ, D = 30 μ.

south-east Africa. Dingle (1981) concluded that *R. nealei*'s preferred habitat was water <100 m deep, where environmental conditions ranged from high to low energy.

Genus *Gibberleberis* Dingle, 1969

Three species of this genus have been recorded, all from the Zululand–Umzamba area of south-east Africa. Two of these (*G. africanus* and *G. elongata*) occur in Santonian strata, and the former ranges down into the Coniacian. Although never abundant, the genus is a characteristic element of the Coniacian–Santonian faunas of south-east Africa. Bate (*in* Bate & Bayliss 1969) recorded a closely allied, monospecific genus from the Upper Turonian of Tanzania: *Akrogmocythere wamiensis*. The author has examined the type specimens in the British Museum (Natural History), and noted that the two genera can be distinguished by the lack of a dorsal margin concavity or neck behind the ACA in *Akrogmocythere*, which also has a distinctly down-turned ATE in the LV hinge. In view of the temporal distribution of the two genera, it is possible that *Gibberleberis* evolved from *Akrogmocythere* in the later Turonian or early Coniacian.

Gibberleberis africanus Dingle, 1969

Fig. 36A–C

Gibberleberis africanus Dingle, 1969: 376–377, fig. 17; 1980: 57, figs 30A–D, 31A.

Remarks

Intraspecific morphological variation within *G. africanus* primarily takes the form of differences in the strength and coarseness of the surface rib pattern. The type populations from Umzamba exhibit distinctly coarser reticulation and stronger muri and main rib patterns than those from Zululand, where material from Richards Bay BH9 borehole and outcrops has a more delicate ornamentation. In addition, the Coniacian examples are somewhat plumper and squatter than younger forms, although I have no hesitation in assigning them to the same species.

Age and distribution

Although never abundant, *G. africanus* is ubiquitous in the Coniacian to Santonian strata of the Zululand–Umzamba area. It ranges Santonian II to Santonian III at Umzamba and the Richards Bay BH9 borehole, and Coniacian IV (locality 15, Mtubatuba) to Santonian III (locality 74, False Bay) at outcrop in Zululand. It is a useful marker for Coniacian–Santonian strata in south-east Africa.

Data from the Richards Bay BH9 borehole suggest that *G. africanus* preferred shallow (<100 m), low-energy, open-water conditions (Dingle 1980).

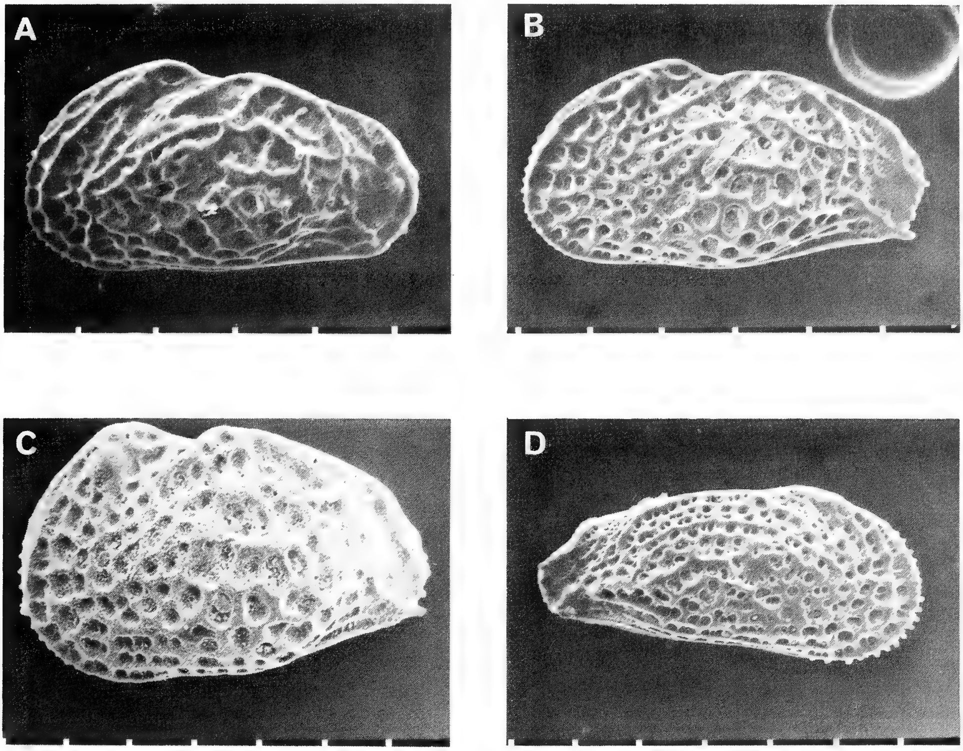


Fig. 36. A–C. *Gibberleberis africanus*. A. SAM–PC6568, LV, Umzamba bed 1, Santonian II, SEM 377. B. SAM–K5658, BH9, Richards Bay, 118,22 m, Santonian III, SEM 395. C. SAM–PC6569, LV, locality 15–7, Coniacian IV, SEM 1947.
D. *Gibberleberis elongata*, SAM–K5660, holotype, BH9 Richards Bay, 124,0 m, Santonian III, SEM 390. Scale bars = 100 μ.

Gibberleberis elongata Dingle, 1980

Fig. 36D

Gibberleberis elongata Dingle, 1980: 57–59, figs 30E–F, 31A; 1981: 111, figs 52D, 53A.

Remarks

This is a relatively rare species, which has not been encountered in Zululand Coniacian–Santonian strata at outcrop.

Age and distribution

Ranges Santonian III to Campanian II in Richards Bay BH9 borehole, and Campanian II at outcrop in Zululand (Nibela Peninsula). It has not been recorded from equivalent strata at Umzamba.

Indeterminate taxa

Indet. sp. 1874

Fig. 37A

Remarks

One poorly preserved carapace of a sub-rectangular, trachyleberid-like species. It has an overall reticulate ornamentation, a nodose dorsal longitudinal ridge, a short ventromedian longitudinal rib, and a large posteroventral spine.

Age and distribution

Santonian III, St. Lucia Formation, locality 74–10, False Bay.

Indet. sp. 1956

Fig. 37B

Remarks

One poorly preserved carapace of a trachyleberid-like species. The carapace narrows posteriorly, and is dominated in the posterior half by three short longitudinal ridges. There is a weak SCT, and an AM ridge. No details of fine surface ornamentation can be seen.

Age and distribution

Coniacian IV, St. Lucia Formation, locality 15–1, Mtubatuba.

Indet. sp. 2078

Fig. 37C

Remarks

One broken valve, probably belonging to *Cytherella*. The outline resembles most closely that of *Cytherella* sp. 2 recorded by Dingle (1980) from the Santonian to Campanian of the Richards Bay borehole.

Age and distribution

Santonian III, bed 5, Umzamba.

Indet. sp. 2103

Fig. 37D

Indeterminate species A Dingle, 1969: 380–381, fig. 20a–c (MG–1–2–1).

Remarks

No additional specimens of this species have been recorded since its original description. SEM photographs emphasize the pseudo-alate ventrolateral ridge.

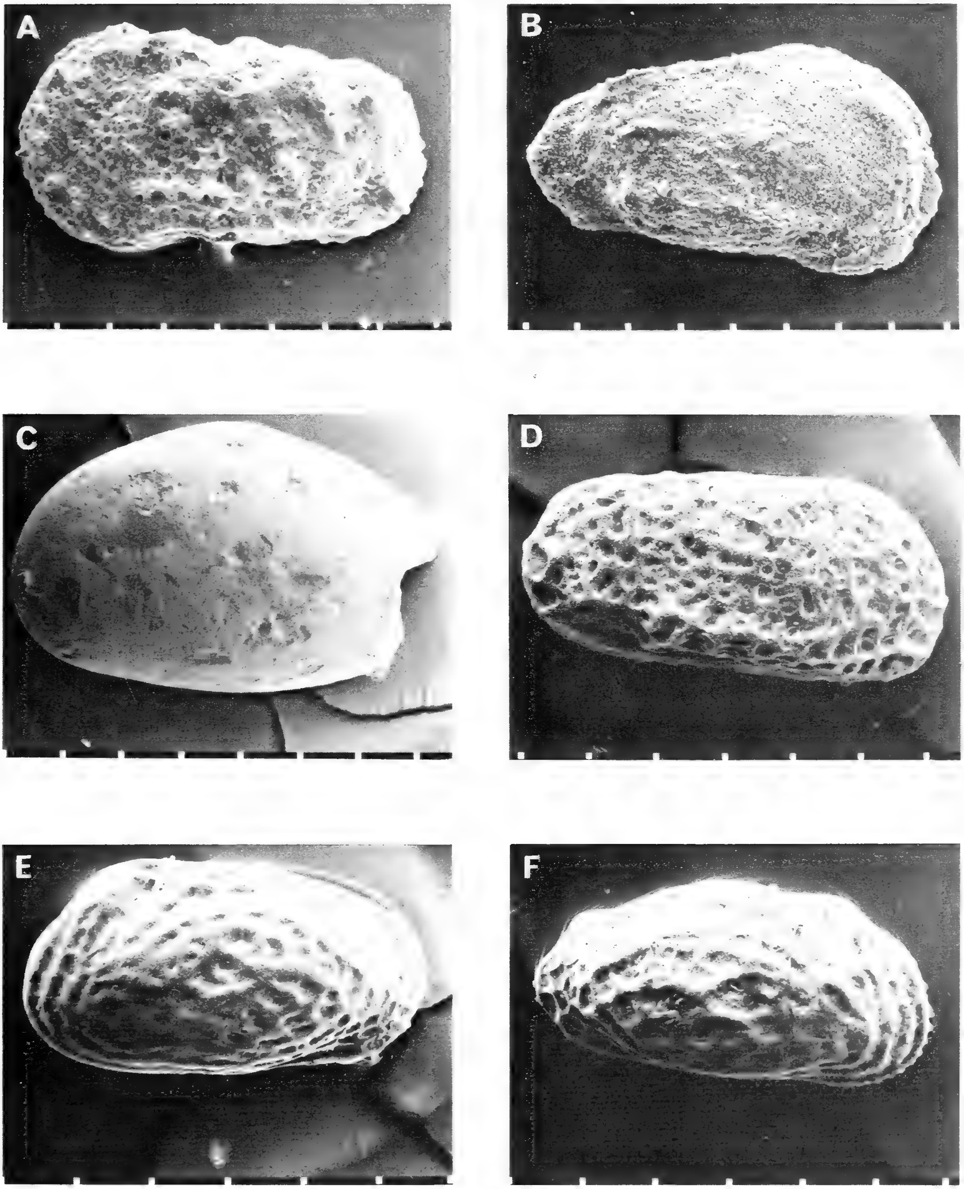


Fig. 37. Indeterminate taxa. A. Indet. sp. 1874, SAM–PC6570, LV, locality 74–10, False Bay, Santonian III. B. Indet. sp. 1956, SAM–PC6571, locality 15–1, Mtubatuba, Coniacian IV. C. Indet. sp. 2078, SAM–PC6572, RV, Umzamba bed 5, Santonian III. D. Indet. sp. 2103, SAM–PC6573, RV, Umzamba bed 1, Santonian II. E–F. Indet. sp. 2104, Umzamba bed 1, Santonian II. E. SAM–PC6574, LV, SEM 2104. F. SAM–PC6575, RV, SEM 2106. Scale bars = 100 μ.

Age and distribution

Santonian II, bed 1, Umzamba.

Indet. sp. 2104

Fig. 37E–F

Indeterminate species B Dingle, 1969: 381, fig. 20d–g (MG–1–2–3a, b).

Remarks

Two worn valves, which show considerable resemblance to *Veenia obesa*. There are, however, significant points of difference: Indet. sp. 2104 lacks a distinctive SCT, and a median lateral ridge, and the CA in both valves are less prominent than in *V. obesa*. There is a superficial resemblance, mostly in valve outline, to *Akrogmocythere wamiensis* from the Turonian of Tanzania (Bate & Bayliss 1969) but Indet. sp. 2104 lacks the prominent DM ridge.

Age and distribution

Santonian II, bed 1, Umzamba.

Indet. sp. 2108

Fig. 38A

Indeterminate species C Dingle, 1969: 381, fig. 20i–h (MG–1–2–4).

Remarks

A relatively well-preserved carapace of an elongate, delicately reticulate species.

Age and distribution

Santonian II, bed 1, Umzamba.

Indet. sp. 2125

Fig. 38B

Remarks

Poorly preserved carapace and single valve of trachyleberid-like species. Both specimens encrusted with matrix, but prominent features observed are: SCT, posteriorly rising nodose ventrolateral ridge, prominent ACA.

Age and distribution

Santonian III, locality 74–12, False Bay.

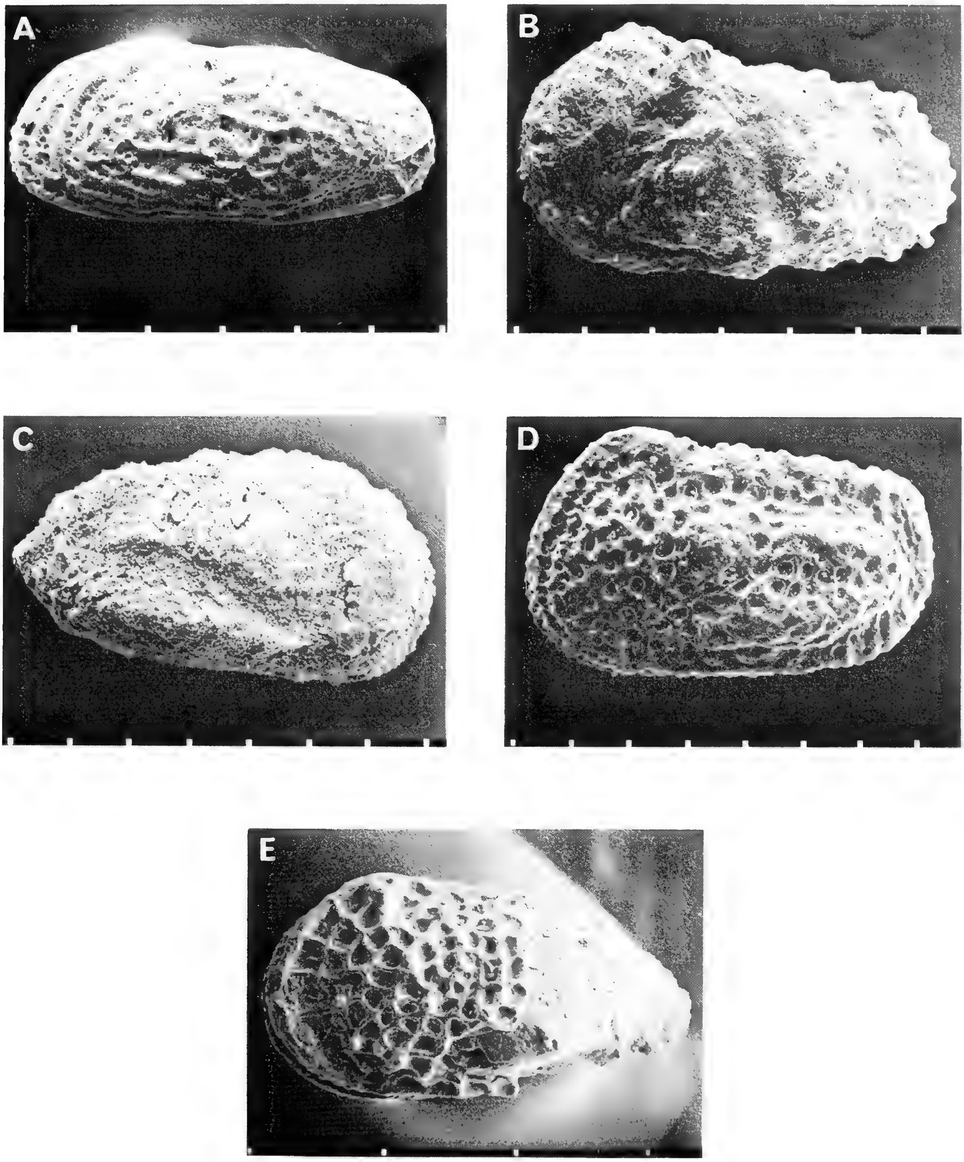


Fig. 38. Indeterminate taxa. A. Indet. sp. 2108, SAM–PC6576, LV, Umzamba bed 1, Santonian II. B. Indet. sp. 2125, SAM–PC6577, LV, locality 74–12, False Bay, Santonian III. C. Indet. sp. 2132, SAM–PC6578, RV, locality 15–1, Mtubatuba, Coniacian IV. D. Indet. sp. 2314, SAM–PC6579, LV, J(c)–1 borehole, 2 213 m, Upper Cenomanian, SEM 2313. E. Indet. sp. 2312, SAM–PC6580, J(c)–1 borehole, 2 213 m, Upper Cenomanian, SEM 2311. Scale bars: A–D = 100 μ, E = 300 μ.

Indet. sp. 2132

Fig. 38C

Remarks

Poorly preserved valve of trachyleberid-like species. Specimen encrusted with matrix, but prominent features observed are: tapering posterior outline, and three short longitudinal ridges in posterior half of valve.

Age and distribution

Coniacian IV, locality 15–1, Mtubatuba.

Indet. sp. 2312

Fig. 38E

Remarks

Fragmented valve of reticulate trachyleberid-like species. Probably possesses a prominent eyespot and conjunctive spines. Superficially similar to some species of *Oertliella*. No closely related species known from Zululand, or J(c)–1 borehole.

Age and distribution

Upper Cenomanian, J(c)–1 borehole, 2 213 m (7 260 ft).

Indet. sp. 2314

Fig. 38D

Remarks

Worn carapace of reticulate cytheracean. In overall shape and ornamentation, this species resembles several members of the genus *Rocaleberis*, which occurs in the Upper Cretaceous (Maastrichtian) of Argentina (e.g. Bertels 1976). Prominent features include: a SCT, three longitudinal ribs, rounded PM and AM, and prominent ACA. No related ostracod species are known from the Cretaceous of southern Africa and the closest correlative may be the record of *Henryhowella* sp. from the Lower Eocene–Upper Oligocene of the J(c)–1 borehole, 1 216–345 m (3 990–1 130 ft) by Dingle (1976). In this regard, the possibility of downhole contamination from younger strata cannot be ruled out.

Age and distribution

Upper Cenomanian, J(c)–1 borehole, 2 213 m (7 260 ft).

DISCUSSION

Fifty-five species of Ostracoda, belonging to at least 20 genera, have been identified from the Turonian, Coniacian, and Santonian strata of south-east Africa, and their temporal and spatial distributions are shown in Tables 1, 11, and 12. In this section, I will first discuss biostratigraphic and palaeoecological aspects of the assemblages from each of the four main areas studied (Zululand, offshore Natal, east coast, and Agulhas Bank), then consider regional correlations, and finally note some implications of ostracod distributions in a Gondwanide setting.

BIOSTRATIGRAPHY AND PALAEOECOLOGY

Zululand

At outcrop in southern Zululand, Kennedy & Klinger (1975) recognized a Coniacian I to Santonian III succession, which is separated from the underlying Cretaceous strata by an uppermost Cenomanian–Turonian non-sequence. The Turonian reported in subcrop by McLachlan & McMillan (1979) occurs farther north. Unfortunately, not all the samples that were collected through the outcrop succession were fossiliferous, but the composite sequence that it has been possible to construct, using material from the Mfolozi Valley, False Bay area, and BH9 at Richards Bay, covers most of Coniacian III to Santonian III time. The main deficiency is lack of data across the Coniacian–Santonian boundary.

Table 11 shows the distribution of ostracods in Zululand, and compares the assemblages from outcrops (Coniacian III to Santonian III) and Richards Bay BH9 (Santonian II to III). Table 12 shows the total time ranges for taxa at both BH9 and outcrop. A total of 34 species in at least 14 genera have been identified from Zululand, with 24 species (12 genera), and 24 species (13 genera) from outcrop and BH9, respectively (Table 11). Fourteen species are common to the two regions (42% similarity, although the latter figure rises to 58% if the Santonian species only are considered).

Palaeoenvironmental analyses have previously been carried out on the Santonian section of the Richards Bay borehole BH9 (Dingle 1980), and the techniques applied in that study have been employed here. In addition, because of the continuous record, and good preservation of the material from this borehole, the results will serve as a standard for comparison. This earlier work need only be summarized here and the results reviewed in the light of new data.

Because of the relatively small numbers of specimens recovered from some of the samples collected at outcrop, and the discontinuous nature of these outcrops, any palaeoenvironmental predictions made from the ostracod populations must be regarded as tentative. The only sections that give a continuous enough record to be of use are those in the Mfolozi Valley (localities 15 and 16), and at False Bay (locality 74), where Coniacian III–IV and Santonian II–III, respectively, are exposed (Figs 2, 3). The ostracod populations of these two areas

Table 11

Distribution of Coniacian to Santonian ostracods in Zululand.

Outcrop							Species	BH9		
Coniacian III (16)	Coniacian IV (89, 15)	Coniacian V	Santonian I	Santonian II (74)	Santonian III (74, 14)	Camp. I		Santonian II	Santonian III	Camp. I
x							*Cythereis mfoloziensis*			
x	x			x	x	x—*	*Brachycythere longicaudata*	x	x	x—*
	x						*Cytherella* sp. 1929			
	x						*Cytherelloidea mtubaensis*			
	x						Indet. sp. 1956			
	x						Indet. sp. 2132			
	x						*Cythereis* cf. *luzangaziensis*			
	x						*Rayneria nealei*	x	x	x
	x			x	x		*Cytherelloidea newtoni*	x	x	
	x				x		*Haughtonileberis haughtoni*	x	x	x
	x			x	x	x—*	*Paracypris zululandensis*	x	x	x—*
	x			x	x		*Gibberleberis africanus*	x	x	
	x			x	x	x—*	*Cythereis klingeri*	x	x	x—*
	x			x	x	x—*	*Bythocypris richardsbayensis*	x	x	x—*
	x			x	x	x—*	*Cytherelloidea umzambaensis*	x	x	x—*
	x				x		*Oertliella pennata*		x	x—*
	x			x	x		*Unicapella stragulata*			
				x			Indet. sp. 2125			
				x	x		*Cytherella* sp. 2351			
				x	x	x	*Paracypris umzambaensis*	x	x	x—*
				x		x—*	*Haughtonileberis fissilis*	x	x	x—*
					x		Indet. sp. 1874			
					x		*Cythereis transkeiensis*	x		
					?x	x—*	*Bairdoppilata andersoni*	x	x	x—*
						x—*	*Brachycythere sicarius*	x	x	x—*
							Cytherella sp. 1–4	x	x	x—*
							Brachycythere pondolandensis	x	x	
							Pondoina sulcata		x	
							Amphicytherura tumida		x	x
							Cytherelloidea gardeni		x	
							Gibberleberis elongata		x	
							Oertliella sp. 476		x	x—*
							Cytherelloidea griesbachi		x	x—*
						x—*	*Haughtonileberis vanhoepeni*		x	x
Species extant:										
2	16			14	16	10	33 Con.–Sant. species 14 genera	16	23	17(+6 Camp. forms)
17			17				42 % similarity 14 spp. common	24		

( ) numbers in parentheses are localities

* = range extends above Campanian I

TABLE 12

Comparison of ranges of ostracods in Zululand (outcrops & BH9) and Umzamba.

Zululand							Species	Umzamba		
Con.			Santonian			Camp.		Sant.		Camp.
III	IV	V	I	II	III			II	III	
x							*Cythereis mfoloziensis**			
x	x			x	x	x	*Brachycythere longicaudata*	x	x	x
	x						*Cytherella* sp. 1929			
	x						*Cytherelloidea mtubaensis**			
	x						Indet. sp. 1956			
	x						Indet. sp. 2132			
	x						*Cythereis* cf. *luzangaziensis**			
	x			x	x		*Cytherelloidea newtoni**			
	x			x	x		*Gibberleberis africanus*	x	x	
	x			x	x	x	*Haughtonileberis haughtoni*	x	x	x
	x			x	x	x	*Rayneria nealei*		x	
	x			x	x	x	*Paracypris zululandensis**			
	x			x	x	x	*Cythereis klingeri**			
	x			x	x	x	*Bythocypris richardsbayensis**			
	x			x	x	x	*Cytherelloidea umzambaensis*	x	x	x
	x			x	x	x	*Oertliella pennata*		x	x
	x			x	x		*Unicapella stragulata**			
				x			Indet. sp. 2125			
				x	x		*Cytherella* sp. 2350			
				x	x		*Brachycythere pondolandensis*	x	x	
				x	x	x	*Cytherella* sp. 1–4*			
				x	x	x	*Paracypris umzambaensis*	x	x	
				x	x	x	*Haughtonileberis fissilis*	x	x	x
				x	x	x	*Bairdoppilata andersoni*		x	x
				x	x	x	*Brachycythere sicarius*		x	
					x		Indet. sp. 1874			
					x		*Cythereis transkeiensis*	x	x	x
					x		*Pondoina sulcata*	x	x	
					x		*Cytherelloidea gardeni*	x	x	
					x		*Gibberleberis elongata**			
					x	x	*Amphicytherura tumida*	x	x	x
					x	x	*Oertliella* sp. 476*			
					x	x	*Cytherelloidea griesbachi**			
					x	x	*Haughtonileberis vanhoepeni**			
							*Brachycythere rotunda***	x		
							Indet. sp. 2103**	x		
							Indet. sp. 2104**	x		
							Indet. sp. 2108**	x		
							*Veenia obesa***	x	x	
							*Paraphysocythere thompsoni***	x	x	
							Cnestocythere? sp. 2091**		x	
							Indet. sp. 2078**		x	
Species extant:										
2	16			19	27	17	42 Con.–Sant. species 36 % similarity	17	19	8
17			28				15 spp. common	23		

* confined to Zululand—13

** confined to Umzamba—8

Richards Bay & Umzamba: 32 spp, 15 common, 47 % similarity

are detailed in Table 13. Plotting these data on a Cytheracea–Cytherellidae–Bairdiacea+Cypridacea triangular diagram (CCBC plot; see Dingle 1980, 1981 for discussion) (Figs 39, 40) reveals several trends that are potentially significant as palaeoecological indicators.

The five Coniacian samples are cytheracean-dominant and cluster towards the top of the diagram close to the fields considered by Dingle (1980) in his study of the Richards Bay borehole BH9 as shallow-water (<100 m), high- and low-energy environments (assemblages 1 and 3) (Fig. 39). The composition of the Coniacian ostracod populations (Table 14) is very similar to that of the Santonian of Richards Bay (Dingle 1980), and similar environments of deposition are inferred. Factors significant in making this comparison are: (i) dominance of *Brachycythere longicaudata, Cythereis klingeri*, and *Haughtonileberis haughtoni*; (ii) dominance of the cytherellid component by species of *Cytherelloidea*; (iii) absence of *Bairdoppilata* in the Bairdiacea+Cypridacea component, which is composed of *Bythocypris* and *Paracypris*. At Richards Bay, the lower-energy environment (assemblage 3) is characterized by the dominance of *Cythereis klingeri*, so it may be possible to differentiate high- and low-energy assemblages within the Coniacian populations on the grounds of variations in the cytheracean element (Fig. 41).

In contrast, the Santonian II and III ostracod populations from the False Bay area plot in areas on the CCBC diagram that are considered predictive of relatively deep water (see Dingle 1981, fig. 75). There appear to be two distinct fields in the assemblages, one of which contains the Santonian II and lower Santonian III populations, and the other with the upper Santonian III populations (Fig. 39). The former lies in a region of the CCBC diagram for which there is no previous documentation, but which borders on field 7 that contained Maastrichtian assemblages that were considered predictive of deep water (>500 m) (Dingle 1981). Spread of the data points within the Santonian II–III field (Fig. 39) may not be significant because some of the samples contain few specimens. Its ostracod population is dominated by bairdiacean/cypridacean forms and, although *Bairdoppilata* is present, it is *Bythocypris richardsbayensis* that is the main element. In this respect, the Santonian II–III assemblages differ significantly from those of the Maastrichtian assemblage that was used to define field 7. Further important differences are the lack of blind cytheraceans, and typical deep-water markers such as *Krithe*. Furthermore, the presence of various cytheracean elements that are dominant in shallow-water assemblages (e.g. *Brachycythere longicaudata, Cythereis klingeri*, and *Haughtonileberis haughtoni*) suggests that the Santonian II–III field represents deposition in water significantly shallower than field 7. However, because of the overall subordination of cytheracean types, it is considered somewhat deeper than fields to the north of the '*Bythocypris*' line. Overall, the characteristics of this field seem closer to those of 4a (which has a predictive water depth of 100–200 m) than 7, and is referred to as 4c; a predictive intermediate water depth of 300 m is tentatively assigned to it.

TABLE 13

Distribution of ostracods from Zululand outcrops, expressed as percentages of total population.

	Coniacian					Santonian								
	III	IV				II	III							
Locality no.	16	15				74	74							
Bed no.	1	1	3	5	7	9	10	10	11	11	12	13	14	15
Subdivision							1	2	1	2				
CYTHERACEA	100	65	100	84	91	35	21	—	33	66	46	47	50	42
Cythereis mfoloziensis	33													
Haughtonileberis haughtoni				10	29		7				15	13		4
Brachycythere longicaudata	66			21	26	16			33		31	27	50	13
Cythereis cf. *luzangaziensis*				2										
Gibberleberis africanus					10	6								17
Rayneria nealei				5	10									
Cythereis klingeri		65	100	40	10	10	7			66				
Oertliella pennata				6	3		7							8
Unicapella stragulata					3	3						7		
CYTHERELLIDAE	—	24	—	10	10	32	14	—	—	33	23	20	—	13
Cytherelloidea mtubaensis		18												
Cytherelloidea newtoni				2		6						13		
Cytherella spp.		6		8		23	14			33	15	7		13
Cytherelloidea umzambaensis					10	3					8			
BAIRDIACEA & CYPRIDACEA	—	12	—	8	—	42	71	100	67	—	31	34	50	42
Bythocypris richardsbayensis		12		5		29	57				31	7	50	17
Paracypris umzambaensis						3		100				27		
Bairdoppilata andersoni														25
Paracypris zululandensis				3		10	14		67					
Smoothed data (3 point means)														
Cytheracea	83	88	83	92	98	26	19	18	33	48	53	48	46	46
Cytherellidae	12	8	11	7	10	21	17	5	11	19	25	14	11	7
Bairdiacea & Cypridacea	6	4	7	3	4	53	71	79	56	49	22	38	42	46
No. valves per sample	3	17	2	63	31	31	14	3	6	3	13	15	8	24

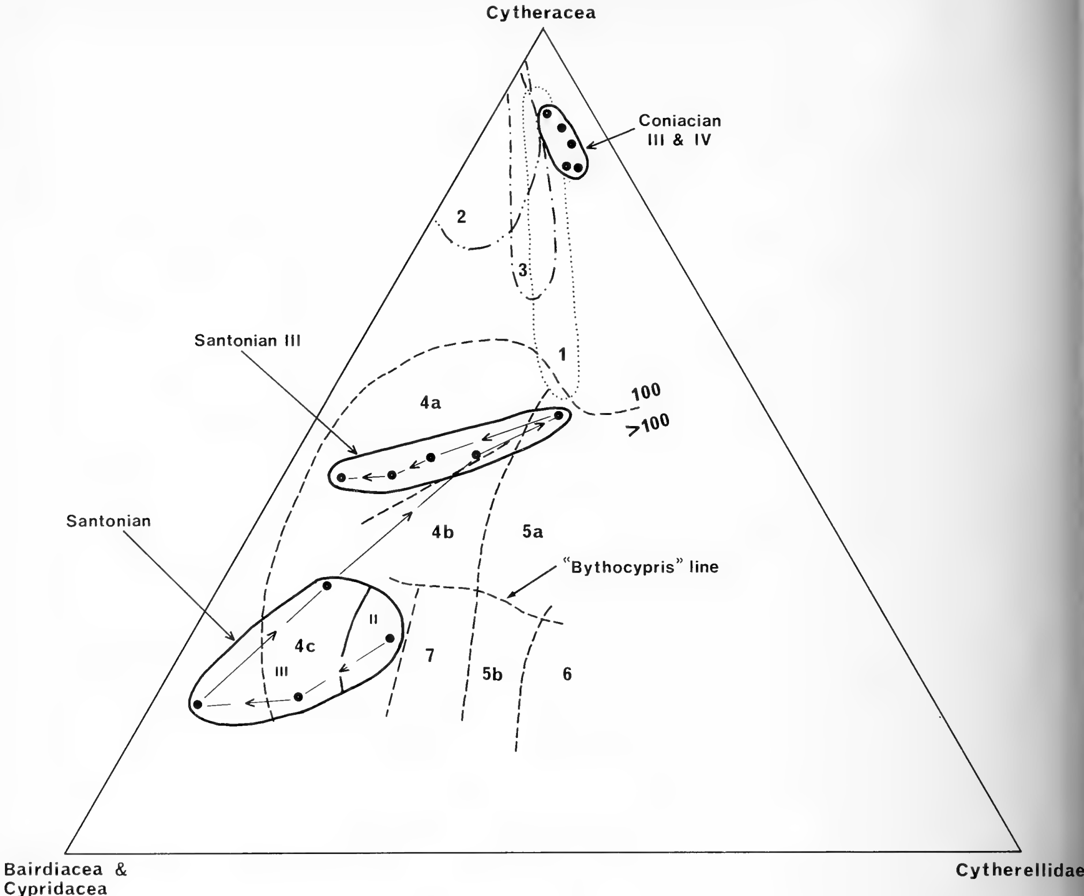


Fig. 39. Cytheracea–Cytherellidae–Bairdiacea+Cypridacea triangular diagram (CCBC plot) of the various populations (solid circles) from the Coniacian to Santonian strata of Zululand. Fields 1, 2, 3, 4a, 4b, 5a, 5b, 6 and 7 have previously been defined by Dingle (1980, 1981). See text for explanation.

The younger Santonian III populations from locality 74 (Table 14) scatter across the CCBC diagram in the vicinity of field 4a (Fig. 39). Comparison with the original ostracod assemblages (Campanian I of BH9) used to establish this field (see Dingle 1981, table 6) shows that the only significant difference is the dominance of *Bythocypris richardsbayensis* in the bairdiacean component of the False Bay samples in contrast to *Bairdoppilata andersoni*, which plays an analagous role in the Richards Bay samples. I have no hesitation in assigning the upper Santonian III populations to this assemblage field and predicting a depositional environment of 100–200 m. Only the position of the sample on the right-hand side of the field is in doubt. It may indicate a temporary water depth shallowing to *c.* 100 m, but because the 'event' is predicted by one sample its

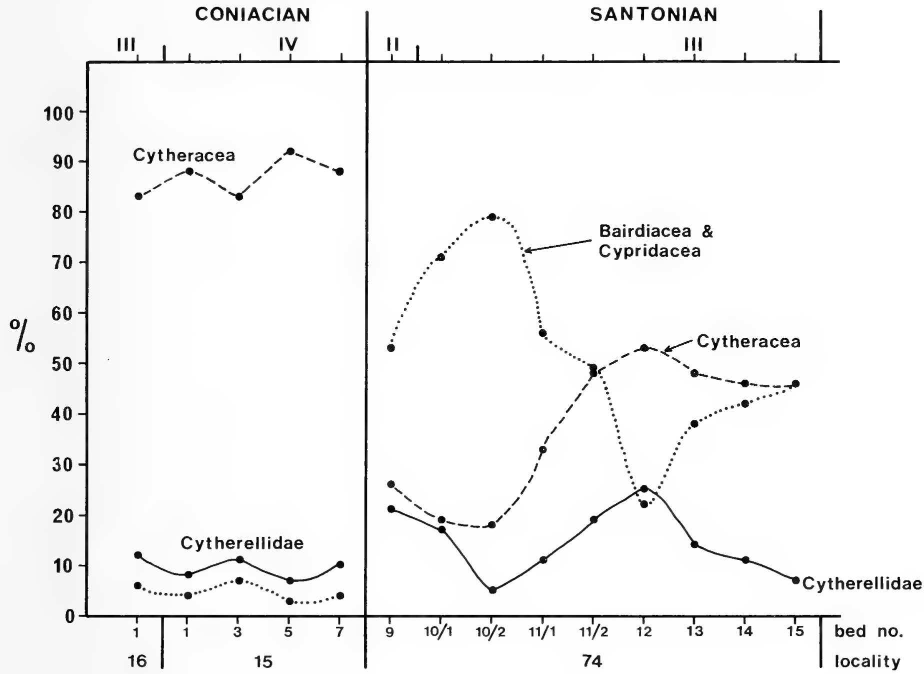


Fig. 40. Temporal trend of major groups (as percentage of total ostracod population) in Zululand outcrops. Data are three-point running means.

significance is difficult to assess, other than to suggest that a somewhat shallower water environment may be located in this field.

Palaeoecological and predicted sedimentary environments for the Santonian section of the Richards Bay BH9 borehole have been fully discussed in Dingle (1980). These data have been incorporated in various figures referred to below.

Dingle *et al.* (1983) have discussed some of the palaeoenvironmental aspects of Upper Cretaceous sedimentation in Zululand, and have stressed the onlapping nature of the Upper Cretaceous transgression that was first recognized by Kennedy & Klinger (1971). The BH9 borehole site lies to the south of the Eteza Fault on the crest of a basement feature referred to as the Richards Bay Arch. Differential vertical movements were recognized between this area and the basin farther north under the Zululand coastal plain. The data acquired during the present study allow modifications to be made to the model presented by Dingle *et al.* (1983).

Figure 42 shows a tentative temporal and spatial correlation of depositional environments along a transect between the False Bay–Nibela Peninsula area, the Mfolozi Valley, and BH9 (100 km in length). The diachronous nature of the post-Turonian transgression is well illustrated, with Coniacian I, Coniacian II,

TABLE 14

Characteristics of Coniacian and Santonian ostracod assemblages from Zululand (Mfolozi Valley and False Bay).

	Coniacian III–IV	Sant. II & Lower Sant. III	Upper Santonian III
Dominant (>20%, >1 sample)	*Brachycythere longicaudata* *Cythereis klingeri*	*Paracypris zululandensis*	*Brachycythere longicaudata* *Bythocypris richardsbayensis*
Secondary (>10%, >1 sample)	*Haughtonileberis haughtoni*	*Brachycythere longicaudata* *Cytherella* sp. *Bythocypris richardsbayensis*	*Haughtonileberis haughtoni* *Cytherella* sp.
Tertiary (>5%, >1 sample)	*Rayneria nealei* *Bythocypris richardsbayensis* *Cytherella* sp.	*Cythereis klingeri* *Paracypris umzambaensis*	*Cytherelloidea newtoni*
Minor (>5%, 1 sample)	*Cythereis mfoloziensis* *Gibberleberis africanus* *Oertliella pennata* *Cytherelloidea mtubaensis* *Cytherelloidea umzambaensis*	*Haughtonileberis haughtoni* *Gibberleberis africanus* *Oertliella pennata* *Cytherelloidea newtoni*	*Bairdoppilata andersoni* *Cythereis klingeri* *Oertliella pennata* *Unicapella stragulata* *Cytherelloidea umzambaensis*
Other features	No *Bairdoppilata* Dominance of *Cytherelloidea* in Cytherellidae	No *Bairdoppilata* Dominance of *Cytherella* in Cytherellidae *Brachycythere longicaudata* is main cytheracean	*Bairdopillata* present
	No. species = 17 Diversity = 15%	No. species = 12 Diversity = 22%	No. species = 15 Diversity = 24%
PALAEOECOLOGY Water depth Equivalent fields on CCBC diagram.	 <100 m 1 & 3	 ?300 m 4c	 100–200 m 4a

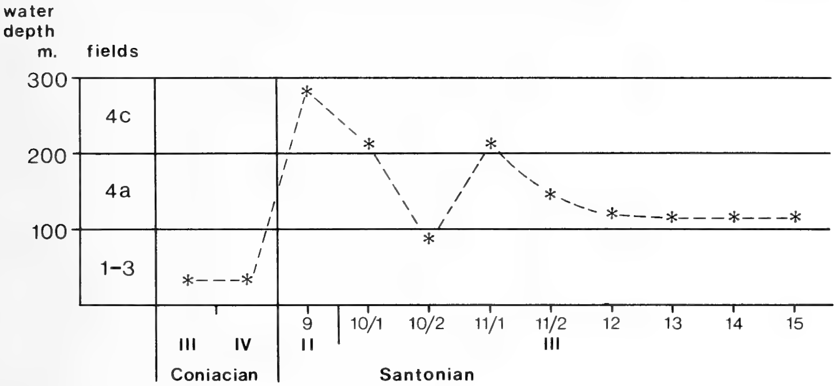


Fig. 41. Summary of predicted temporal water-depth variations at Zululand outcrops based on the CCBC plot in Figure 39. Coniacian localities are in the Mfolozi Valley; Santonian locality (74) is at False Bay. Bed numbers are shown on horizontal axis. Age decreases to the right.

and Santonian II basal sediments at the three localities, respectively, although fossiliferous samples were available only from the first two sites. Despite their age differences, both have very similar ostracod faunas that are characterized by robust cytheraceans *Brachycythere longicaudata, Haughtonileberis haughtoni*, and *Cythereis klingeri*. At BH9, where there is a continuous cored section, the Santonian II to Campanian II sequence appears to show an uninterrupted progression from shallow- (<100 m), through medium- (100–200 m), to deep-(>300 m) water sedimentary environments. Farther north, in the Mfolozi Valley, I have no data to establish the Coniacian V to Santonian I palaeoenvironments, but suspect that it also represents a progression from shallow (Coniacian III–IV), through medium (Campanian II to III), to deep (Campanian IV) water conditions. This correlation suggests that similar sedimentary conditions to those that prevailed during the uppermost Santonian III to mid-Campanian II medium water-depth environments in BH9 were established over the Mfolozi Valley area for the whole of the Coniacian V or Santonian I to lowermost Campanian IV time span.

Information from the False Bay Nibela Peninsula area is less complete. It is reasonable to assume that the earliest sedimentary environment (Coniacian I) was also shallow water, high energy, so that similar ostracod populations to those found at the two southerly sites can be anticipated here. However, I cannot substantiate this assumption. Higher in the sequence, conditions cannot be predicted, and the available data are not easy to assess because only short pre-upper Campanian sections contained ostracod faunas. In particular, the upper Santonian II–III section commences with a relatively deep-water (300 m) ostracod assemblage that is immediately overlain by medium (100–200 m) water-depth assemblages assigned to field 4a on the CCBC diagram. The simplest

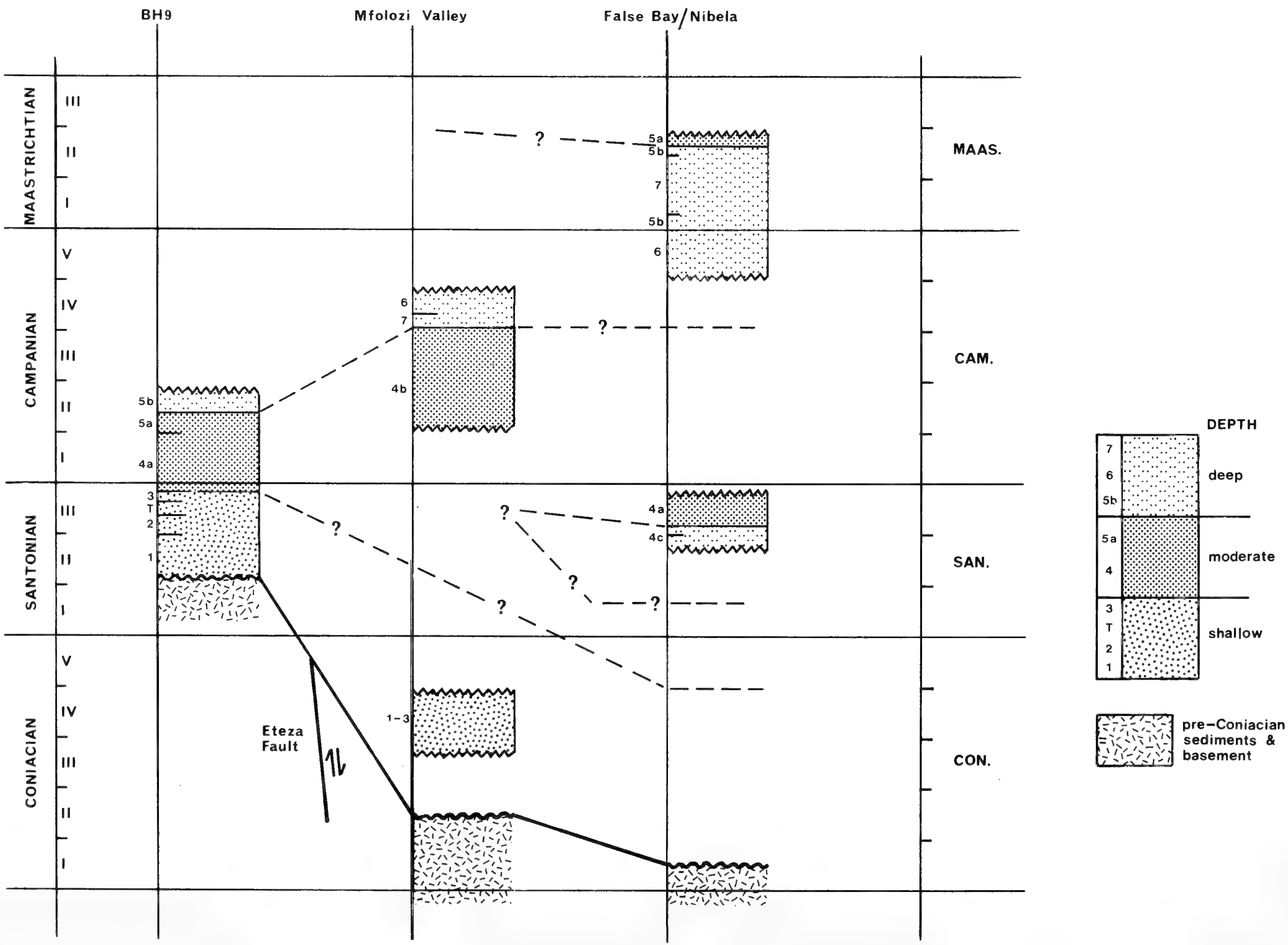


Fig. 42. Temporal and spatial water-depth variations in the Coniacian to Maastrichtian strata of Zululand from the Richards Bay borehole (BH9) (south) to the False Bay–Nibela area (north). Small numbers at left side of columns are fields on CCBC plots (Dingle 1980, 1981, this paper).

correlation (Fig. 42) is that this represents a deep-water episode that may not have penetrated as far south as the Mfolozi area, although critical data around the Coniacian–Santonian boundary are lacking. Deep-water environments were definitely established in the Nibela area by late Campanian times, and, with some fluctuation, persisted until the rapid shallowing that commenced in Maastrichtian II. The diachronous nature of these major sedimentary environmental changes is well illustrated in Figure 42: the shallow–medium boundary ranges from north to south (?late Coniacian to ?early Santonian to latest Santonian) and the medium–deep water boundary ranges south to north (mid-Campanian II to lower Campanian IV to ?Campanian IV).

Considering these data in terms of water-depth curves (Fig. 43) suggests that the sedimentary environments shown on Figure 42 cannot be explained simply in terms of eustacy. Dingle *et al.* (1983) have predicted differential vertical movements between the Richards Bay Arch and the region lying to the north, and in particular, that during Campanian I–II times, the crest of the arch (i.e. BH9 site) subsided more rapidly than the basin to the north (water depths at this time were greatest over the arch). The new data also suggest that once the Mfolozi area had subsided to an approximate water depth of 100–200 m (by Coniacian IV), it remained at this depth until early Campanian time. This presumably resulted from one, or a combination, of the following: eustatic still-stand and no sediment accumulation, sediment accumulation at the same rate as a sea-level rise, crustal subsidence and sediment accumulation compensating for either a eustatic sea-level rise or still-stand. Because there is no evidence for either abnormally thick sediments, or temporally extensive condensed sequences, I favour a slow sediment-accumulation rate coupled with a slow eustatic sea-level rise. This raises a further ambiguity in the False Bay area, where relatively deep-water conditions were followed by shallowing that coincided with the inundation of the Richards Bay Arch. The attainment of deep-water conditions at the northernmost site,

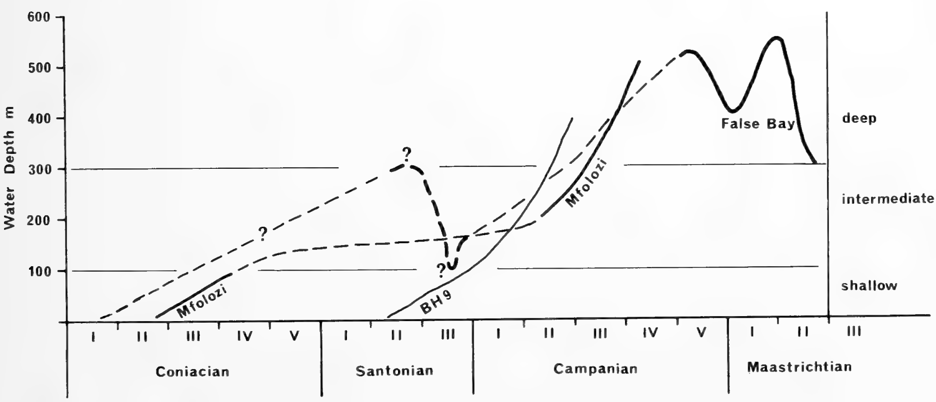


Fig. 43. Water-depth fluctuations during the Upper Cretaceous transgression at three Zululand localities. Based on the CCBC plot (Fig. 39) and Dingle (1980, 1981).

which experienced the transgression earliest, is not difficult to envisage if a faster rate of crustal subsidence compared to the Mfolozi area obtained here, but the Santonian III shallowing suggests either crustal uplift of 100–200 m, rapid sedimentation outstripping the rising sea level effectively elevating the sea floor, or a combination of slight crustal uplift and a moderate increase in the sediment-accumulation rate. Since a period of slow sea-level rise (in the Mfolozi Valley) during Santonian to early Campanian time has already been postulated, the option of an increase in the sedimentation rate perhaps coupled with a decrease in crustal subsidence seems most attractive. As noted earlier, the non-coincidence of the more regularly curved portions of the graphs during early Campanian time strongly suggest that differential crustal movements and sediment accumulation rates must be anticipated over the whole of this region.

In Zululand 34 species have been recognized from Coniacian–Santonian strata, with 17 each from Coniacian and Santonian outcrops, and 24 from the Santonian of BH9. Because of their good state of preservation and completeness of the record, the ranges obtained from BH9 are probably more reliable. Tables 11 and 12 show the ranges of the ostracod species by stages, following the ammonite zonation scheme of Kennedy & Klinger (1975), while Table 15 shows species that are confined to each stage, and Table 16 lists the order of appearance of important Upper Cretaceous species.

It is clear from these data that despite the relative sparseness of many of the assemblages, which in some cases at least was occasioned by poor preservation, the Coniacian ostracod populations contained most of the main elements that characterized later Upper Cretaceous faunas. This indicates that these long-ranging taxa aggressively colonized the continental margins of south-east Africa as soon as local circumstances allowed, following the initiation of the Upper Cretaceous transgression. Table 16, for instance, shows that 14 per cent of the Maastrichtian taxa appeared in the Coniacian, and that this figure grows rapidly to 36 per cent for the Santonian. Prominent in this list are species that form significant components of the overall post-Coniacian populations: *Brachycythere longicaudata, Cythereis klingeri, Haughtonileberis haughtoni*, and *Bythocypris richardsbayensis*. Only four additional long-ranging species joined the list during Santonian time. It can be established, therefore, that the underlying character of the Upper Cretaceous faunas was established rapidly after the Cenomanian–Turonian hiatus, and was not acquired over a long period of time.

Only three species (20%) are confined to the Zululand Coniacian strata (Table 15), two of which are closely related. One (*Cythereis* cf. *luzangaziensis*) is likened to a species from the Turonian of Tanzania, and the other (*Cythereis mfoloziensis*) may be ancestral to the long-ranging *Cythereis klingeri*. None of these three short-range species have been found to occur abundantly, and at this state of knowledge it is not possible to identify taxa that indicate unequivocally a Coniacian, in contradistinction to a Santonian, age. Reliance has to be placed on the fact that certain other taxa, typical of the younger strata, do not occur.

TABLE 15

Age ranges of Coniacian and Santonian ostracods in south-east Africa.

Zululand	Agulhas Bank
Restricted to Coniacian	
Cythereis mfoloziensis	*Apateloschizocythere?* cf. *mclachlani*
Cytherelloidea mtubaensis	*Brachycythere agulhasensis*
Cythereis cf. *luzangaziensis*	

Zululand	Umzamba
Restricted to Santonian	
Cythereis transkeiensis	
Brachycythere pondolandensis	*Brachycythere pondolandensis*
Pondoina sulcata	*Pondoina sulcata*
Cytherelloidea gardeni	*Cytherelloidea gardeni*
Gibberleberis elongata	
	Brachycythere rotunda
	Paracypris umzambaensis
	Veenia obesa
	Gibberleberis africanus
	Paraphysocythere thompsoni
	Brachycythere sicarius
	Cnestocythere? sp. 2091
	Rayneria nealei
	Indet. sp. 2103
	Indet. sp. 2104
	Indet. sp. 2108
	Indet. sp. 2078

TABLE 16

Rates of appearance of Zululand ostracod species.

Long-range species appearing in: Coniacian		Santonian	
Brachycythere longicaudata	(–Maas.)	*Cythereis transkeiensis*	(–?Maas.)
Cythereis klingeri	(–Maas.)	*Brachycythere sicarius*	(–Maas.)
Bythocypris richardsbayensis	(–Maas.)	*Haughtonileberis fissilis*	(–Maas.)
Cytherella sp. 1–4	(–Maas.)	*Bairdoppilata andersoni*	(–Maas.)
Paracypris zululandensis	(–?Maas.)		
Rayneria nealei	(–Camp.)		
Haughtonileberis haughtoni	(–Camp.)		
Oertliella pennata	(–Camp.)		
Cytherelloidea umzambaensis	(–Camp.)		

Zululand species extant in:	Percentage appearing in: Coniacian	Santonian
Maastrichtian	5/37 = 14%	9/37 = 24%
Campanian	9/40 = 23%	20/40 = 50%
Santonian	12/33 = 36%	

(upper limits shown in parentheses)

Twenty-six species have been recorded from the Santonian of Zululand, 24 of which occur at BH9, and only 17 farther north. Seventeen of these range into the Campanian, where they constitute 50 per cent of the fauna of that stage. In contrast to the Coniacian, there are two relatively well-represented species that are confined to this stage in Zululand, and which are potentially useful stage indices (Table 15): *Brachycythere pondolandensis* and *Pondoina sulcata*, although both have been recorded so far only from BH9. It is possible that their distribution is climatically controlled because they are more abundant farther south at Umzamba, and this aspect will be discussed later in a regional context. Similarly, there are several other species that are typical of Santonian III strata at BH9 (though not confined to them) that do not occur, or are poorly represented farther north: viz. *Amphicytherura tumida, Cytherelloidea griesbachi, Gibberleberis elongata* and *Haughtonileberis vanhoepeni*.

Considering the Coniacian–Santonian fauna of Zululand as a whole, several species appear to be characteristic of the combined stages (Table 12): *Cytherelloidea newtoni, Gibberleberis africanus*, and *Unicapella stragulata*. The last-named is the earliest-known representative of the subfamily Unicapellinae.

Umzamba

Twenty-three species of ostracods have been recorded from the Santonian strata at Umzamba, eight of which (35%) are restricted to the area (Table 12).

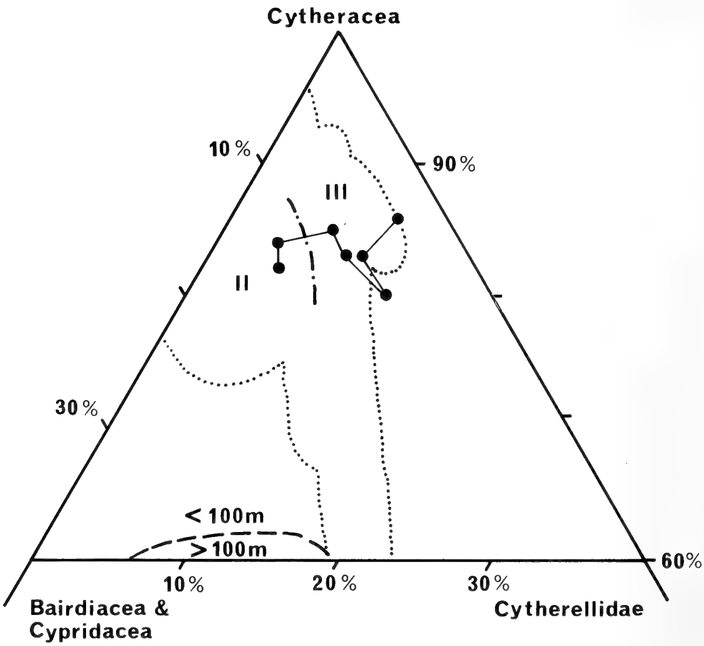


Fig. 44. CCBC plot of Santonian II and III ostracod populations with more than 20 specimens from Umzamba. The data points are joined in ascending order.

This high percentage of endemism gives the Umzamba faunas a distinctive compostion. Because the younger sediments at the Umzamba outcrops are partly decalcified, data on the extension of ostracod ranges into Campanian strata are probably incomplete, but what information there is suggests that several species are confined to the Santonian. This assemblage is considered to be a marker for the 'southern' (Umzamba) Santonian ostracod faunas: *Brachycythere pondolandensis, Pondoina sulcata, Cytherelloidea gardeni, Veenia obesa*, and *Paraphysocythere thompsoni*. The last two species are known only from the Umzamba area and, because they occur relatively abundantly, are particularly useful elements.

Figure 44 shows the ostracod populations (with >20 specimens) from Umzamba plotted on a CCBC diagram. All the samples plot within the shallow-water (<100 m) field and there may be a subdivision between the Santonian II and III populations: the former lie to the left side of the diagram within the field of assemblage 2 from BH9 (Dingle 1980), while the latter lie within the areas overlapped by assemblages 1 and 3 and those from the Zululand outcrops. These data indicate that the Santonian assemblages at Umzamba were deposited in shallow water, with Santonian II possibly having restricted circulation that modified to more open environments higher up the sequence. They also show that the depositional environments at Umzamba during Santonian II and III were similar to those that obtained in Santonian II and III at Richards Bay, and Coniacian III and IV in the Mfolozi Valley.

Borehole J(c)–1

Table 4 shows the distribution of ostracods in the lower part of the J(c)–1 borehole. Two aspects are immediately apparent: the overall sparsity of the fauna (42 valves from 25 available samples, only 12 of which contained ostracods), and the relative lack of cytheracean specimens (12 valves, 29% of total fauna). In addition, many of the carapaces are fragmented, and only 50 per cent of the fossiliferous samples contain more than one carapace. These limitations make any palaeoecological assessment speculative.

The following associations may be significant:

1 981–2 042 m (Santonian)—relatively diverse zone with *Bairdoppilata, Bythocypris, Dutoitella,* and *Cytherella*.

2 054–2 103 m (Santonian–Coniacian)—barren of ostracods, abundant *Inoceramus* prisms and pyrite crystals.

2 115–2 140 m (Coniacian–Turonian)—sparse fauna of *Cytherella* and indeterminate smooth forms.

2 152–2 201 m (Turonian–uppermost Cenomanian)—zone with *Krithe* and *Bairdoppilata*, and indeterminate forms.

2 213–2 237 m (Upper Cenomanian)—zone with cytheraceans, *Bairdoppilata, Bythocypris*, and two indeterminate smooth forms.

2 249–2 297 m (Upper Cenomanian to base of borehole)—zone barren of ostracods except for one pyritic cast of possible *Cytherella*.

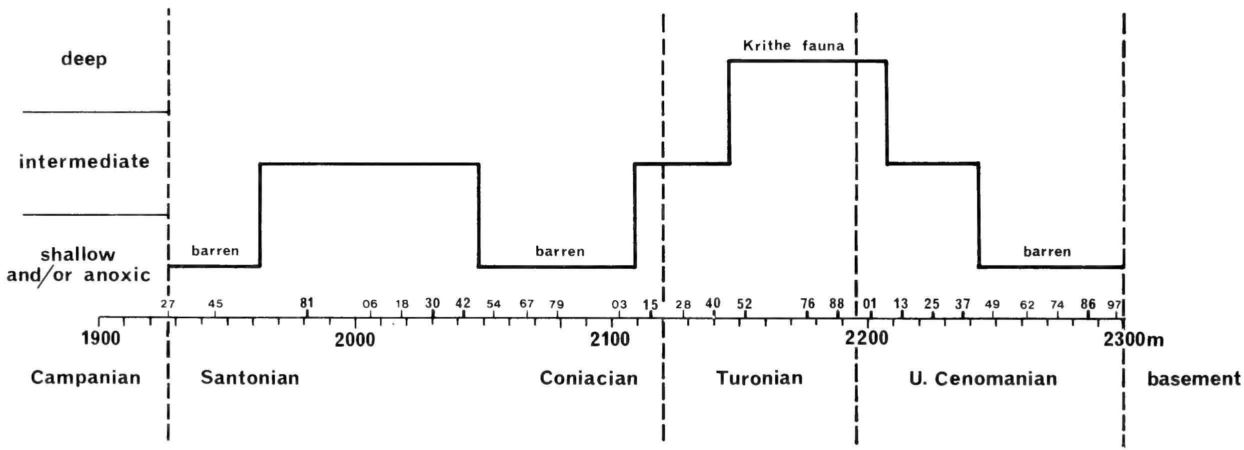


Fig. 45. Speculative environments of deposition and water depth in the lower part of the J(c)–1 borehole. Barren zones are taken to indicate anoxic and/or shallow (i.e. hyposaline) water. *Krithe*-bearing horizons denote relatively deep water, and other faunas are intermediate. Horizontal axis indicates depth downhole in metres, with picked horizons noted above the line (bold numbers indicate ostracod-bearing samples).

The presence of planktonic foraminifera throughout the sequence indicates that the Tugela delta top was connected to the open ocean, but the alternations of barren sequences and the intermittent presence of freshwater charophytes, and a zone with *Krithe* suggests that water depths fluctuated in the manner shown in Figure 45. The two barren sections (2 054–2 103 m and 2 249–2 297 m) are separated by a zone containing *Krithe*, above and below which lie zones containing sparse faunas. The barren sequences may indicate very shallow water (with strong hyposaline characters) and/or periods of anoxic bottom conditions, while the zone with *Krithe* probably indicates moderately deep water (?200 m, see Dingle 1981). This succession may reflect a period of progressively deepening water from Upper Cenomanian to a peak in early–mid-Turonian times, followed by a shallowing and/or decrease in oxygen content of bottom waters, that culminated in the Coniacian barren episode. The Santonian sequences suggest intermediate water depths that possibly shallowed at the end of the period and remained so into the early Campanian (see Dingle 1981, fig. 73). The paradox in this interpretation is that the predicted maximum water depths on the Tugela delta top occur during the Turonian, when evidence from Zululand indicates a withdrawal of the sea and the formation of a major mid-Cretaceous non-sequence. If this interpretation is valid, then the implication is that subsidence on the Tugela delta top was greater than any regional sea-level fall.

Agulhas Bank

Although the Coniacian samples dredged from the Agulhas Bank contained a variety of mollusca, their ostracod faunas were sparse: two species only in sample TBD 510 (*Apateloschizocythere?* cf. *mclachlani* and *Brachycythere agulhasensis*). The former species is close to *A. mclachlani* from the Campanian III of Zululand, but *B. agulhasensis* is distinct from the *Brachycythere* faunas farther north. The paucity of the Agulhas Bank fauna prevents any meaningful biostratigraphic comparisons. From their study of the *Inoceramus* shells, Klinger *et al.* (1980) concluded that the Coniacian depositional environment at site TBD 4510 lay on the inner shelf, with low sedimentation rates and moderately strong bottom currents. This site was only 20 km from site TBD 510, so similar conditions may have obtained during the deposition of the ostracod valves, although we have no additional data to substantiate this possibility.

REGIONAL CONSIDERATIONS

SOUTH-EAST AFRICA

The Coniacian to Santonian ostracod faunas of south-east Africa are of great interest because they document the history of recolonization after the widespread mid-Cretaceous (late Cenomanian–late Turonian) hiatus. The significant dichotomy in the ostracod faunas across this event was recognized by Dingle (1982), but at that time no taxonomic studies had been made on the Coniacian faunas. In this section various aspects of regional biostratigraphy and palaeo-

ecology will be discussed, primarily comparing and contrasting the Umzamba and Zululand regions.

Ostracod zonation

Sufficient data are now available to attempt a preliminary zonation of the Santonian strata of south-east Africa using their ostracod faunas (Fig. 46). Because of regional contrasts in the overall ostracod populations (discussed below), three schemes are needed to effect correlation across the whole Umzamba to False Bay region. The schemes will be defined, then discussed.

Umzamba

***Veenia obesa* Zone**—restricted to early Santonian II. *Definition*: period marked by the presence of *Veenia obesa*, and ending with the first appearance of *Brachycythere pondolandensis* with *Gibberleberis africanus*. *Remarks*: carries a relatively limited fauna that is dominated by *Brachycythere longicaudata*, *Haughtonileberis haughtoni*, and *Pondoina sulcata*, with rare *Brachycythere rotunda*.

***Gibberleberis africanus–Brachycythere pondolandensis* Zone**—range mid-Santonian II to mid-Santonian III. *Definition*: period marked by the presence of *Gibberleberis africanus* together with *Brachycythere pondolandensis*. *Remarks*: can be divided into two subzones. The upper limit is not well controlled between two widely spaced sampling horizons.

***Cytherelloidea gardeni* Subzone**—range mid-Santonian II to early Santonian III. *Definition*: period marked by the presence of *Gibberleberis africanus* with *Brachycythere pondolandensis* and *Cytherelloidea gardeni*. *Remarks*: lowermost part of this subzone coincides with the appearance of several important species: *Cytherelloidea umzambaensis, Cythereis transkeiensis, Paraphysocythere thompsoni*, and *Haughtonileberis fissilis*. Towards the top, *Oertliella pennata* and *Brachycythere sicarius* first appear.

Un-named Subzone—restricted to mid-Santonian III. *Definition*: period marked by the presence of *Gibberleberis africanus* with *Brachycythere pondolandensis* above the last appearance of *Cytherelloidea gardeni*. *Remarks*: during this period, *Veenia obesa* and *Paraphysocythere thompsoni* reach the top of their range, while the local first appearances of *Rayneria nealei* and *Bairdoppilata andersoni* are recorded.

***Amphicytherura tumida* Zone**—range late Santonian III to Campanian (upper limit not known). *Definition*: period marked by the presence of *Amphicytherura tumida* above the last appearance of the *Gibberleberis africanus–Brachycythere pondolandensis* combination. *Remarks*: no species are known to make their appearance in this zone, but the last appearances of *Pondoina sulcata* and *Rayneria nealei* occur near the top.

Richards Bay borehole BH9

***Cytherelloidea newtoni* Zone**—restricted to early Santonian II. *Definition*: period marked by the presence of *Cytherelloidea newtoni*, and ending with the appearance of the *Gibberleberis africanus–Brachycythere pondolandensis* combination. *Remarks*: carries a restricted fauna of *Brachycythere longicaudata, Paracypris* spp., and rare *Cythereis transkeiensis*. At the top of the zone *Cytherella* sp. and *Rayneria nealei* make their local appearance.

***Gibberleberis africanus–Brachycythere pondolandensis* Zone**—range mid-Santonian II to mid-Santonian III. *Definition*: period marked by the presence of *Gibberleberis africanus* together with *Brachycythere pondolandensis*. *Remarks*: carries a diverse fauna, with first appearances of several important species in the lower part. Characterized by the presence of *Brachycythere longicaudata, Rayneria nealei*, and *Cythereis klingeri*. The local range of *Pondoina sulcata* coincides with the lower part of this zone.

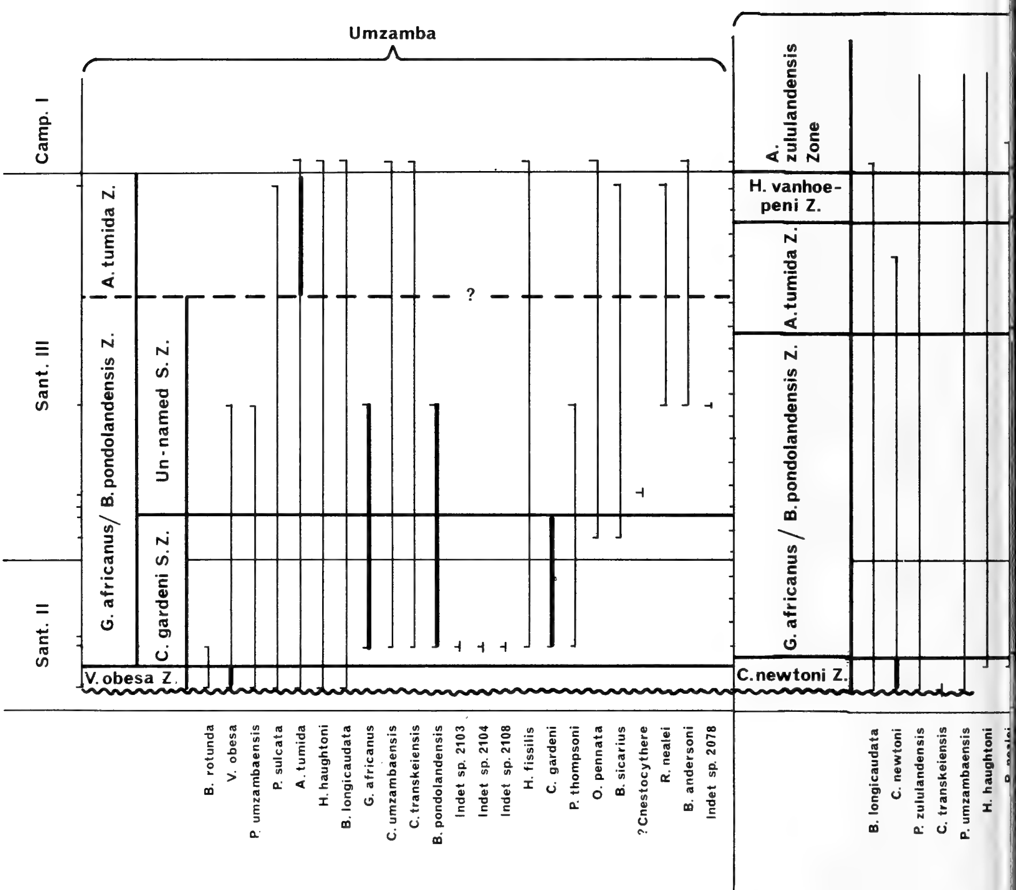
***Amphicytherura tumida* Zone**—range mid- to late Santonian III. *Definition*: period marked by the presence of *Amphicytherura tumida* between the last appearance of *Gibberleberis africanus* with *Brachycythere longicaudata* and the first appearance of *Haughtonileberis vanhoepeni*. *Remarks*: no species are known to make their appearance in this zone, but it includes the upper local ranges of *Cytherelloidea newtoni* and *Gibberleberis africanus*.

***Haughtonileberis vanhoepeni* Zone**—range late Santonian III. *Definition*: period that begins with the appearance of *Haughtonileberis vanhoepeni* and ends with the first appearance of *Amphicytherura zululandensis*. *Remarks*: the upper boundary of this zone probably coincides with the Santonian III–Campanian I boundary. This short zone has no short-range species, but is marked by the appearance of *Gibberleberis elongata* and *Oertliella* sp. 476.

Zululand outcrops

Because of the relative sparseness of the faunas and the relatively few outcrops involved in this study, it has not been possible to devise a satisfactory zonal scheme for this area, either internally, or for correlation with regions to the south. As a preliminary measure, almost the whole Coniacian IV–Santonian III sequence has been placed in one zone, which can be subdivided as more data become available.

***Gibberleberis africanus–Unicapella stragulata* Zone**—range mid-Coniacian IV to late Santonian III. *Definition*: period marked by the presence of *Gibberleberis africanus* together with *Unicapella stragulata*. *Remarks*: only the presence of *Unicapella stragulata* distinguishes this zone from rocks of similar ages farther south, while the remainder of the fauna, with *Brachycythere longicaudata, Haughtonileberis haughtoni* and *Cythereis klingeri*, has a similar content to that in the BH9 borehole.


Umzamba
Camp. I
Sant. III
Sant. II
A. tumida Z.
G. africanus/ B. pondolandensis Z.
Un-named S. Z.
C. gardeni S. Z.
V. obesa Z.
?
B. rotunda
V. obesa
P. umzambaensis
P. sulcata
A. tumida
H. haughtoni
B. longicaudata
G. africanus
C. umzambaensis
C. transkeiensis
B. pondolandensis
Indet sp. 2103
Indet sp. 2104
Indet sp. 2108
H. fissilis
C. gardeni
P. thompsoni
O. pennata
B. sicarius
?Cnestocythere
R. nealei
B. andersoni
Indet sp. 2078
A. zululandensis Zone
H. vanhoe-peni Z.
A. tumida Z.
G. africanus / B. pondolandensis Z.
C. newtoni Z.
B. longicaudata
C. newtoni
P. zululandensis
C. transkeiensis
P. umzambaensis
H. haughtoni

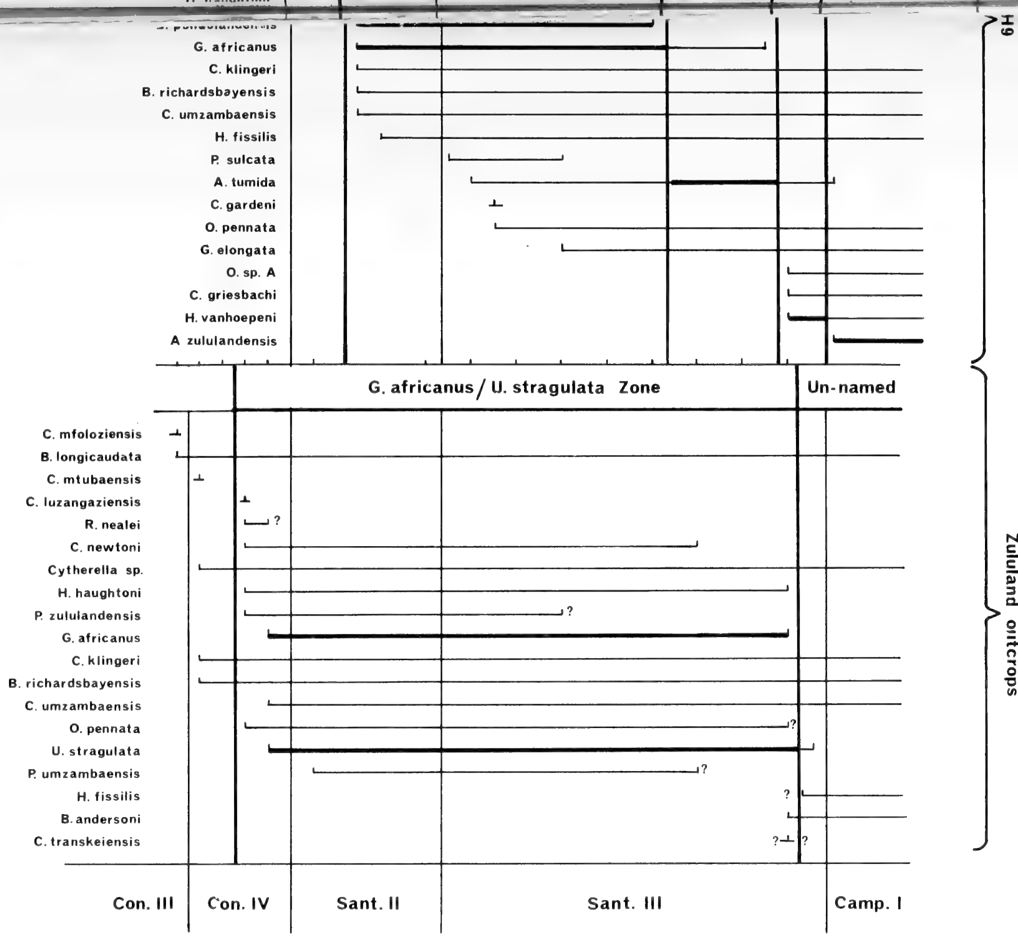


Fig. 46. Basis of proposed ostracod zonation at Umzamba, BH9 (Richards Bay), and the Zululand outcrops in the Mfolozi Valley and False Bay areas. Bold vertical lines indicate zonal boundaries, and bold species ranges are those used in defining zone limits. Ticks on horizontal lines at the top of each locality indicate position of ostracod-bearing samples relative to ammonite zones.
Z = Zone, S.Z. = Subzone.

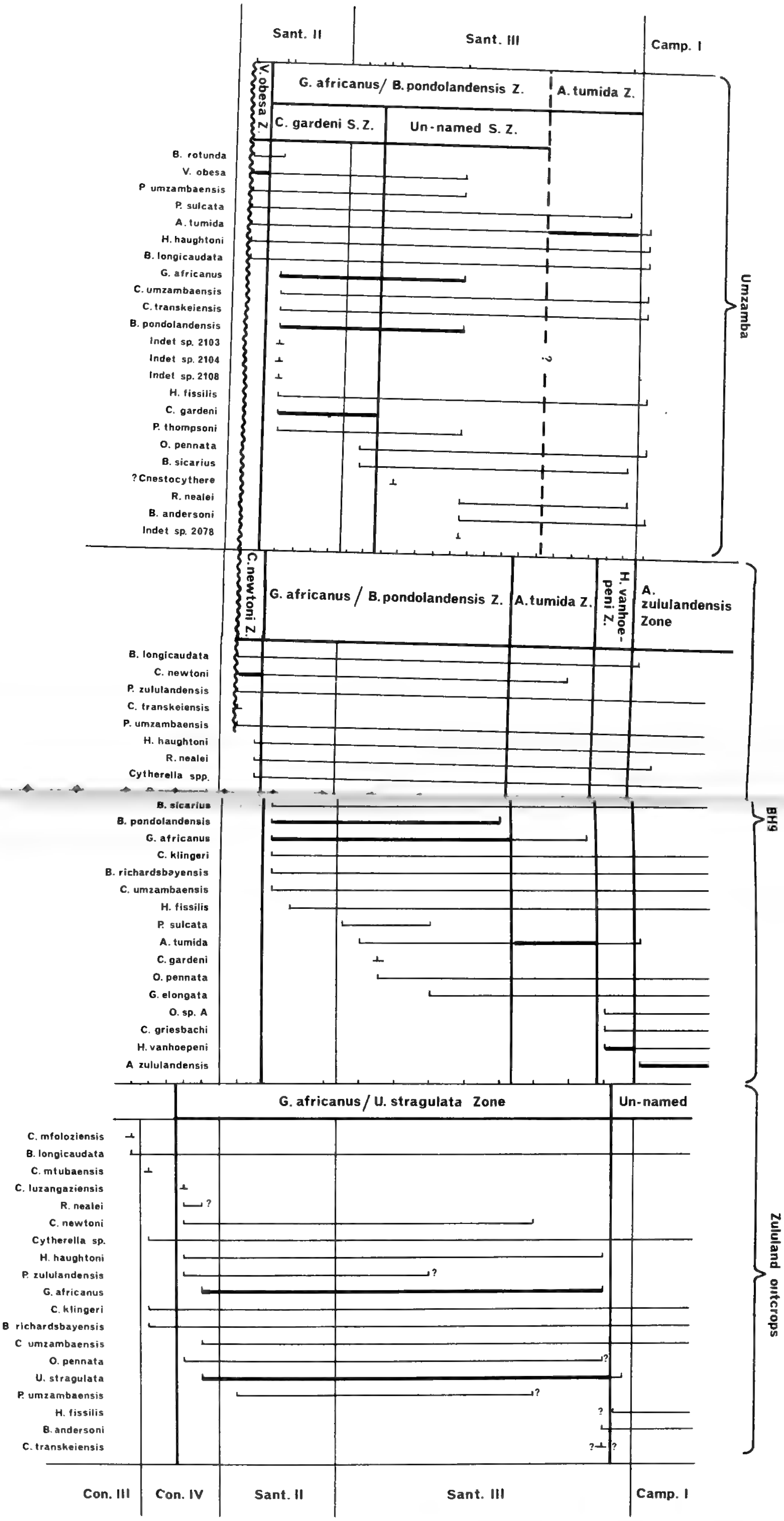


Fig. 46. Basis of proposed ostracod zonation at Umzamba, BH9 (Richards Bay), and the Zululand outcrops in the Mfolozi Valley and False Bay areas. Bold vertical lines indicate zonal boundaries, and bold species ranges are those used in defining zone limits. Ticks on horizontal lines at the top of each locality indicate position of ostracod-bearing samples relative to ammonite zones.
Z = Zone, S.Z. = Subzone.

Figure 47 summarizes the ostracod zonal scheme for south-east Africa defined above and set out in Figure 46. The most complete zonation is that for the Richards Bay area (BH9), where four zones have been recognized in the Santonian II–III sequence. Although the base of this sequence is unconformable on Pre-Cambrian granite, so that it is not possible to define the base of the lowermost zone (*Cytherelloidea newtoni* Zone), its upper limit is probably laterally synchronous with that of the *Veenia obesa* Zone at Umzamba. This is because at both localities the primary control on the range of the overlying *Gibberleberis africanus–Brachycythere pondolandensis* Zone is the vertical distribution of the latter species and I am confident that the range of this species in both areas is very similar, particularly its level of appearance (Fig. 46). North of BH9, in the region of the Zululand outcrops, the *Cytherelloidea newtoni* Zone must be time-equivalent with part of the *Gibberleberis africanus–Unicapella*

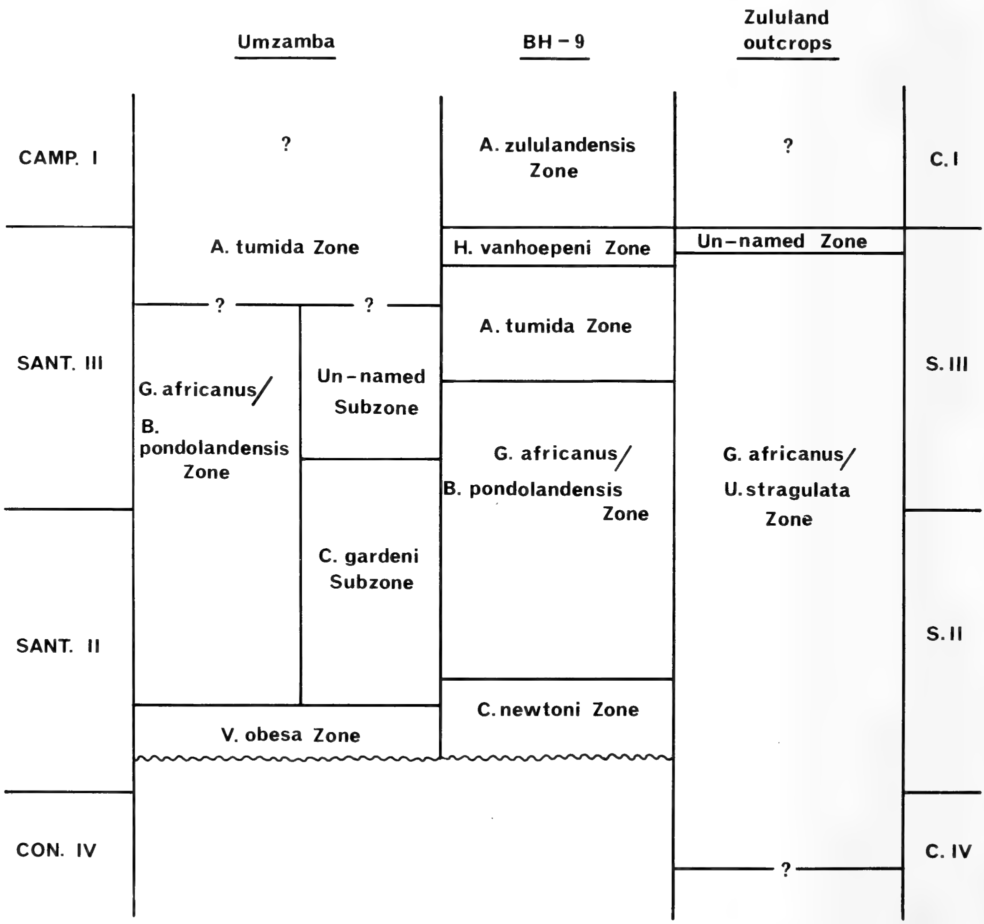


Fig. 47. Summary of ostracod zonation at Umzamba, BH9 (Richards Bay), and Zululand outcrops, and correlation with the ammonite zonation of Kennedy & Klinger (1975).

stragulata Zone, but because *Brachycythere pondolandensis* has not been recognized this far north, the equivalence cannot be assessed.

The upper limit of the *Gibberleberis africanus–Brachycythere pondolandensis* Zone appears to be lower in Santonian III at BH9 than at Umzamba. However, because the samples that control the boundary at Umzamba are widely spaced, this difference may be more apparent than real. In either case, the zone can be correlated between the two faunas because the species used to define it do not appear to be climatically controlled. At Richards Bay, the late Santonian III strata can be placed in a short zone whose upper limit probably coincides with the Santonian–Coniacian boundary (*Haughtonileberis vanhoepeni* Zone). This seems to provide a useful marker between the two stages. Unfortunately, no similar zone can be recognized at either of the other two localities, because sufficiently comprehensive ostracod assemblages from local Campanian I strata are not yet available. At Umzamba I believe that the establishment of two subzones in Santonian II–mid-Santonian III strata will provide additional refinement to age determinations using ostracods. Although a northward extension of the lowermost (*Cytherelloidea gardeni* Subzone) cannot yet be recognized, the one record of the species at Richards Bay does place the relevant horizon at the upper boundary of the subzone in terms of height above the ammonite-defined Santonian II–III boundary.

At present, no satisfactory zonation can be effected for the Coniacian strata in the Zululand outcrops, although the Coniacian IV outcrops have been included in the one zone defined for this area. In particular, the potentially useful species that have been recognized in Coniacian III samples are not yet well enough known to define their ranges.

J(c)–1 and Agulhas Bank

Borehole J(c)–1 lay on the Tugela delta top (Du Toit & Leith 1974; Dingle 1981), approximately 80 km south-west of the Richards Bay area. Despite this geographical proximity, there is a striking dissimilarity between the faunas from the two areas, with no species common. This is particularly so in the cytheraceans, where no genera are common. The presence of *Bythocypris* cf. *richardsbayensis* suggests that there may have been limited contact between the delta top and the Zululand area to the north-east, but the appearance of *Krithe* in the uppermost Cenomanian and Turonian provides further evidence that the sedimentary environments of the areas were markedly different (the earliest record of *Krithe* in the Richards Bay–Zululand area is in Campanian IV of the Mfolozi Valley). Dingle (1981) recognized a similar dichotomy between the two areas in Campanian–Maastrichtian strata, so that the present study indicates that differences in the ostracod faunas were established at the earliest point in the sedimentary history of the delta, and were maintained throughout the remainder of the Cretaceous period.

The two indeterminate cytheraceans (Indet. sp. 2314 and Indet. sp. 2312) in the uppermost Cenomanian apparently have no close relatives either in Zululand

or higher up in the J(c)–1 borehole. Indet. sp. 2314 is superficially similar to *Rocaleberis*, a genus that is first recorded from the Lower Maastrichtian of Argentina, and which is believed to have evolved into the widespread Tertiary taxon *Henryhowella* (Bertels 1976). Until more specimens of Indet. sp. 2314 are available, it is not possible to evaluate any potential relationships, but the palaeogeographic implications for any link of this sort with Argentina would be considerable. The presence of *Dutoitella mimica* in the Santonian extends the lower range of this species, and of the genus in J(c)–1 where it has previously been recorded from the Campanian (Dingle 1981). This confirms a faunal link between the outer Tugela delta top and the Agulhas Bank, which Dingle (1981) detected in Campanian and Maastrichtian strata, and further emphasizes the isolation of the J(c)–1 faunas from Zululand and Umzamba (Fig. 48).

Climatic control

Figure 48 shows the distribution of 24 species of Santonian ostracods between Umzamba, Richards Bay (BH9), and outcrops in Zululand. Previous analyses (Dingle 1980) have suggested that sedimentary environments at the first two sites were similar (Shallow water, <100 m) during Santonian II and III times, so in these cases like is being compared with like. Farther north, where conditions during this period were probably somewhat deeper (200–300 m), comparisons are less meaningful.

Of the 32 species recorded from Umzamba and Richards Bay, 15 are common. Although some of these species are rare and indeterminate, a similarity factor of only 47 per cent between populations of the same age, deposited under similar conditions, and which for the most part are well preserved and well represented, seems significantly low. Table 17 lists the species that are common and restricted to the two areas. Including species which do occur in the other area, but which are rare and restricted in range, 26 per cent of the Umzamba and 38 per cent of the Richards Bay faunas can be considered characteristic of their respective areas. The species that are ubiquitous constitute 43 and 42 per cent of the Umzamba and Richards Bay faunas, respectively. These two faunas are listed here as 'high'- and 'low'-latitude assemblages (the distance is 2,9 degrees). A significant provincialism has also been recorded in the ammonite faunas from the two regions (Klinger & Kennedy 1980).

In assessing the possible causes for this Cretaceous faunal partition, it is necessary to consider the physical setting of the two areas. They lie 320 km apart along a relatively straight coast on which the main intervening feature during early Upper Cretaceous times was the Tugela Delta whose top probably projected seaward, causing an easterly bulge in the coastline (Dingle 1981, fig. 72; Dingle *et al.* 1983, figs 145–146; this paper Fig. 51). Richards Bay lay in the vicinity of a relatively buoyant basement structure (Richards Bay Arch), which was inundated by the Upper Cretaceous transgression in Santonian II times. The modern coastline of Zululand bulges farther eastwards (caused by outbuilding of Upper Cretaceous and Tertiary sediments), but is essentially similar (Fig. 49).

TABLE 17

Spatial distribution of ostracods in south-east African Santonian strata and suggested climatic tolerances. Indeterminate species not shown.

UMZAMBA high latitude 'cool' water 26% of total		ZULULAND low latitude 'warm' water 38% of total	
confined	extends north but rare	extends south but rare	confined
Paraphysocythere thompsoni ***Veenia obesa*** *Brachycythere rotunda*	*Cythereis transkeiensis* *Pondoina sulcata* ***Cytherelloidea gardeni***	*Bairdoppilata andersoni*† *Rayneria nealei*	***Cytherelloidea newtoni*** *Cythereis klingeri* ***Haughtonileberis vanhoepeni*** *Cytherelloidea griesbachi*** *Bythocypris richardsbayensis* *Paracypris zululandensis* ***Unicapella stragulata**** *Gibberleberis elongata***
13% total spp.			29% total spp. in BH9
Ubiquitous, 'intermediate'			
	Gibberleberis africanus *Brachycythere sicarius* *Brachycythere longicaudata* ***Brachycythere pondolandensis***** *Haughtonileberis haughtoni*	*Haughtonileberis fissilis* *Oertliella pennata* ***Amphicytherura tumida***** *Cytherelloidea umzambaensis* *Paracypris umzambaensis*	
43% spp. at Umzamba, 42% spp. at BH9			

* = Zululand outcrops only
** = BH9 only
† = probably water-depth control
Bold type = zone fossil

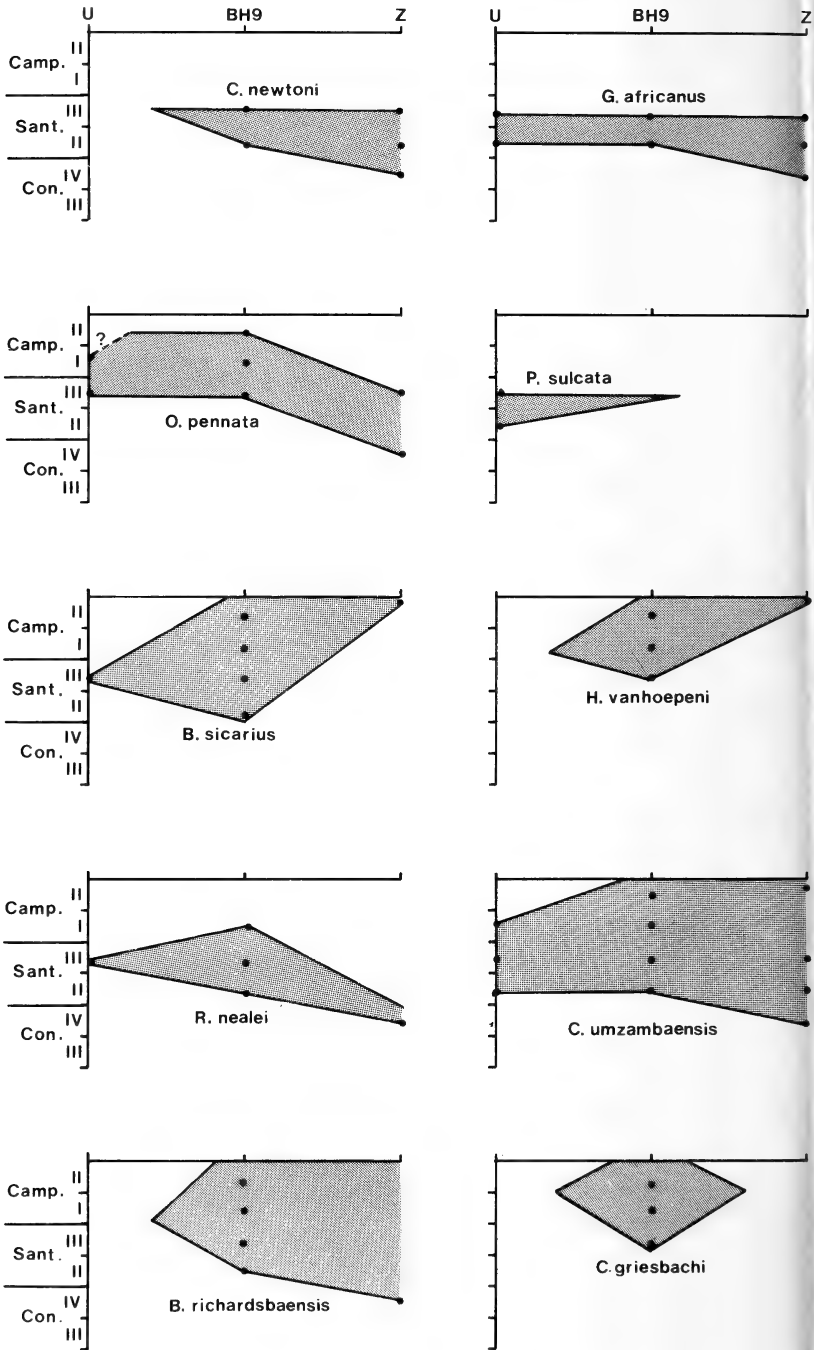
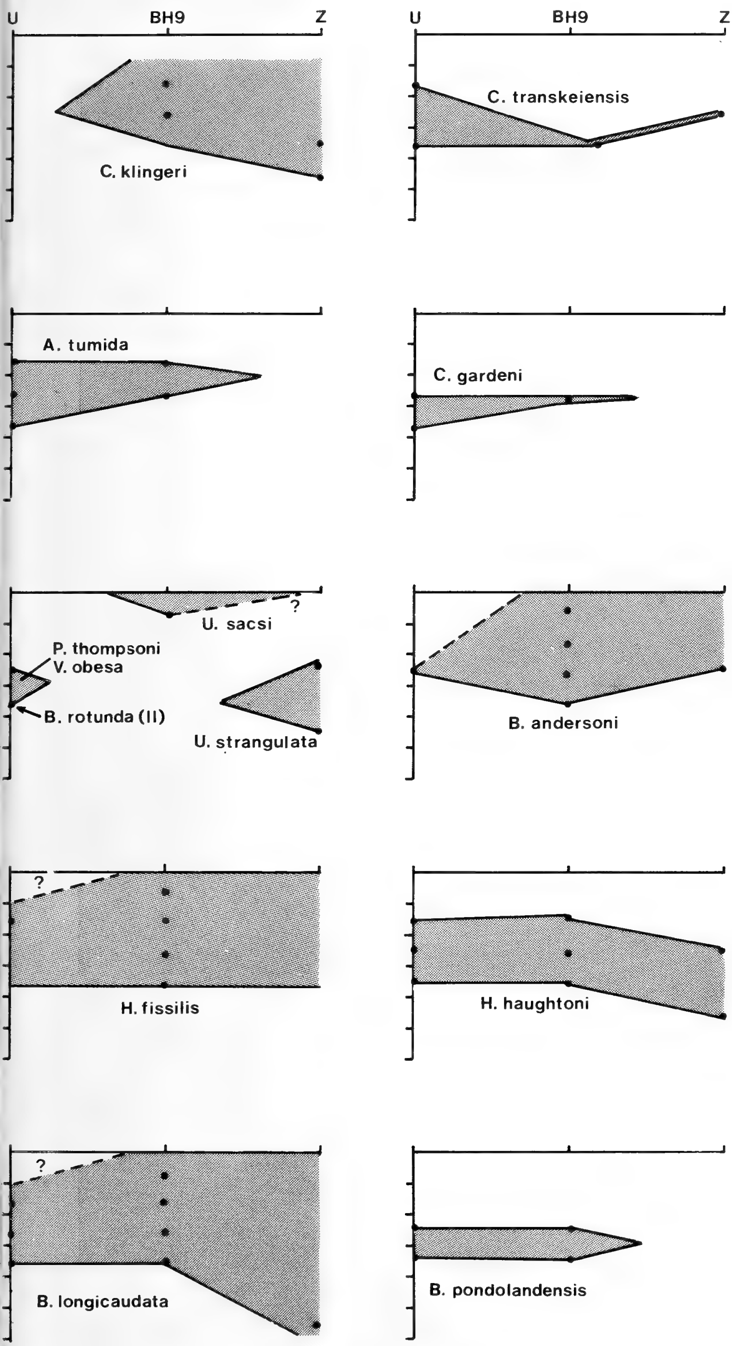


Fig. 48. Temporal distribution of 24 selected species of ostracods between Umzamba (U), Richards Bay (BH9), and the Zululand outcrops in the Mfolozi Valley and False Bay (Z).


U
BH9
Z
C. klingeri
U
BH9
Z
C. transkeiensis
A. tumida
C. gardeni
U. sacsi
?
P. thompsoni
V. obesa
B. rotunda (II)
U. strangulata
B. andersoni
?
H. fissilis
H. haughtoni
?
B. longicaudata
B. pondolandensis

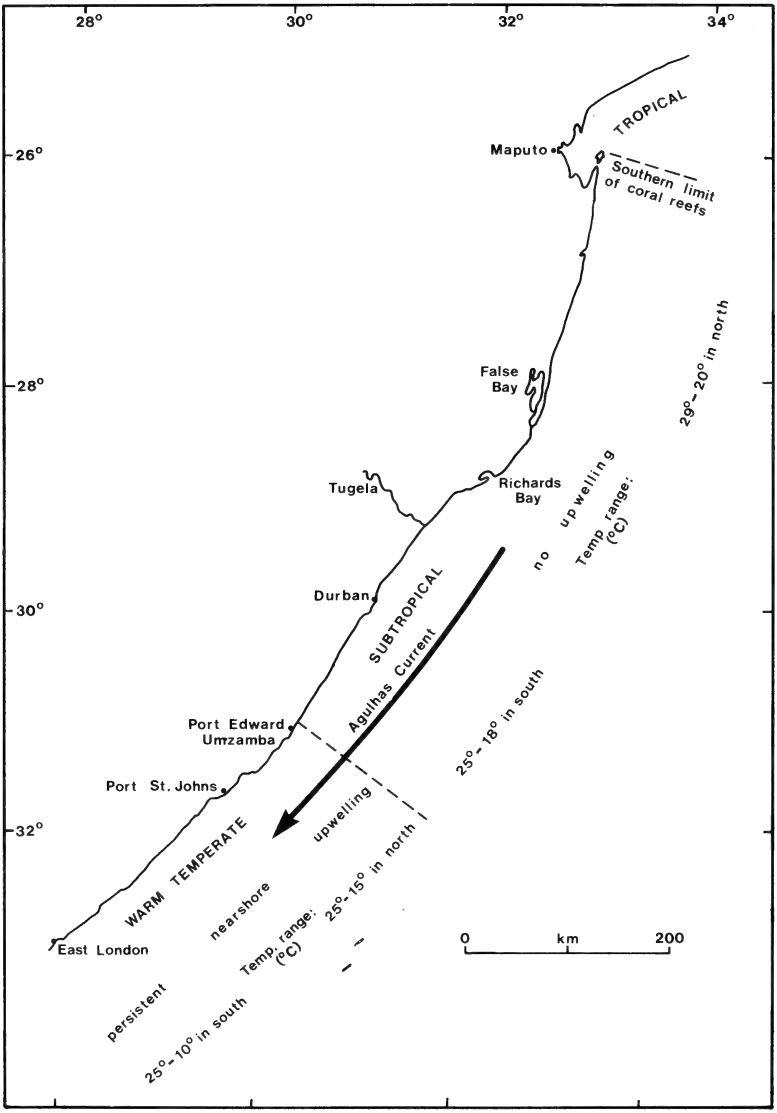


Fig. 49. Modern biogeographical zones of the south-east African coast (Brown & Jarman 1978). Inshore water-temperature data and upwelling characteristics are from Schumann (pers. comm. 1983).

Therefore, there seem to have been no significant physical barriers, beyond those which exist today, to free migration between the two areas, a presumption that is strengthened by the fact that over 40 per cent of each fauna is ubiquitous. Consequently, I surmise that the factors controlling the faunal distribution were related to water-mass properties, e.g. temperature, salinity, and turbidity.

Biogeographical studies of the modern coastal biota have identified three marine provinces along the south-east coast: tropical, subtropical, and warm temperate (Brown & Jarman 1978), with the boundary between the last two lying in the vicinity of 31°S latitude (about 10 km north of Umzamba, Fig. 49). The limiting factor between the subtropical and warm-temperate provinces seems to be the mean minimum water temperatures (see Brown & Jarman 1978), which south of 31°S range 10–15 °C, and north of 31°S range 18–20 °C (see Fig. 49 for further details of inshore water temperatures, which were supplied by E. Schumann (National Research Institute of Oceanology, Stellenbosch, pers. comm. 1983)). This suggests that the faunal discontinuity is related to a difference of 6–7 °C in the mean minimum water temperatures. The key factor here is the occurrence of persistent nearshore upwelling south of Port Edward (just south of 31°S) (E. Schumann, pers. comm. 1983) that modifies the relatively high temperatures of the south-west flowing Agulhas current (up to 25 °C at 31°S). No data are available on the distribution of modern Ostracoda, but these boundaries are clearly defined in the distribution of important taxa such as corals and molluscs.

Comparisons with the present situation cannot be taken far because elements of the oceanographic circulation, in which the western-boundary Agulhas Current is dominant, have not been identified earlier than mid-Tertiary (e.g. Martin 1981), although Haq (1981) has suggested that it was in existence by early Palaeocene times. A speculative Cretaceous palaeocirculation was discussed by Gordon (1973, fig. 4), who predicted a north-east or east-north-eastward flowing current along the south-east coast of Africa in Santonian times, based on the assumption of a more poleward location of the equivalents of the modern southern-oceans low-pressure atmospheric cells. Recently, Barron & Washington (1982) have modelled various atmospheric parameters using a mid-Cretaceous (100 m.y.) global palaeogeography, and concluded that in fact the reverse situation is likely to have occurred: low-pressure cells were located over the oceans adjacent to the southern portions of South America, Africa, and Madagascar–India. In Figure 50 we have used this distribution to speculate on wind and ocean currents. Because south-east Africa lay within the westerly wind belt and a southern-ocean return current can be expected between 55° and 60°S, an eastward-flowing ocean current is predicted along the northern part of the mid-Cretaceous southern ocean, with an east-north-east component off the coast of south-east Africa. This is in fact what Gordon (1973) suggested (for different reasons), although I do not anticipate a major southerly current into the palaeo-Mozambique Channel as he did. It is also similar to that produced from palaeogeographical considerations by Lloyd (1982), and numerically modelled by

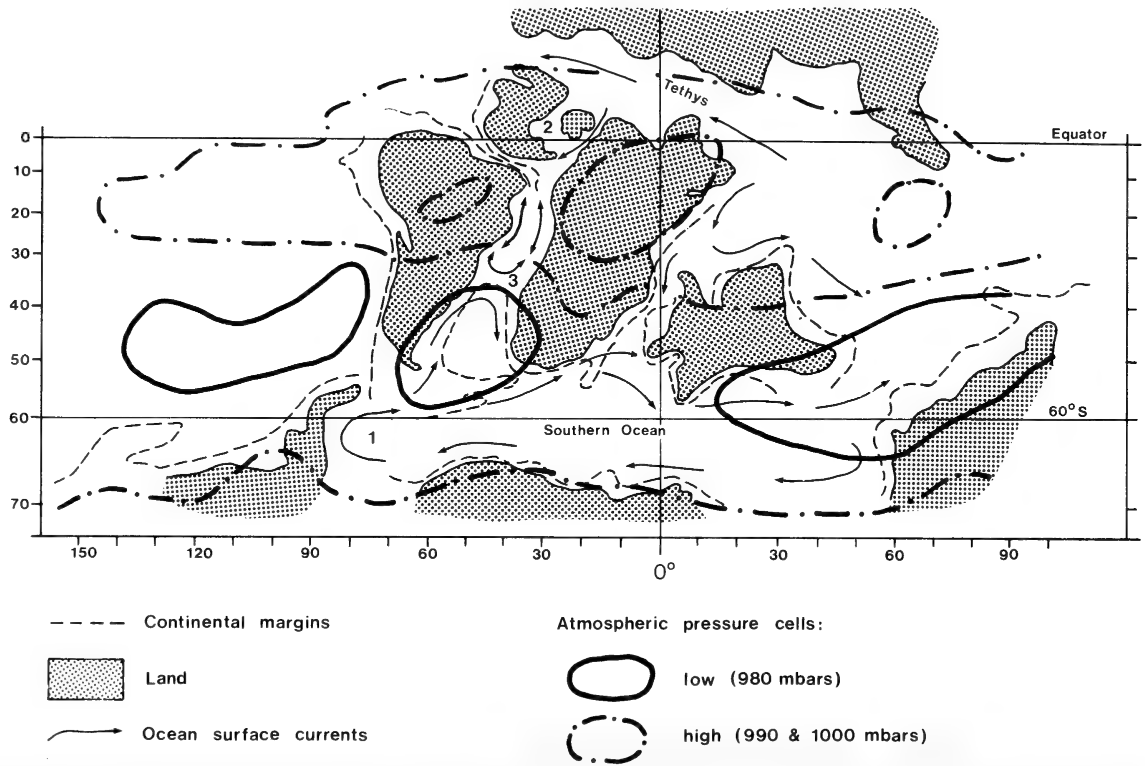


Fig. 50. Southern, South Atlantic, Tethys, and south-west Indian ocean surface water currents in mid-Cretaceous times. Based on the atmospheric pressure modelling and palaeogeography of Barron & Washington (1982). 1 = Southern Ocean retroflexion resulting in a return current. 2 = Temporary trans-Saharan seaway, with currents flowing southward from Tethys. 3 = Narrow northern sector of the South Atlantic, possibly with a monsoonal (reversing) pattern. Zululand lies approximately 50°S 25°W.

Seidova & Yenikeev (1983). Some modification of Barron & Washington's (1982) 100 m.y. model will be necessary for early Santonian time (say 82 m.y.) but the essential geographical features were still in existence at this time, so probably no significant ocean-circulation changes had occurred: a narrow South Atlantic and Southern Ocean; the close proximity of India and Madagascar to Africa; and continuity of a South American–Antarctic–Australasian landmass. In Figure 51 a palaeogeographical sketch of the Umzamba–Richards Bay area in Santonian times is shown, with a north-east flowing offshore current (East Coast Current). Barron & Washington (1982, fig. 2) predict a mean annual range of approximately 12–22 °C in surface temperatures in the vicinity of coastal south-east Africa for mid-Cretaceous times, in comparison with regional averages of 15–24 °C at present (*Times Atlas* 1980). Coastal upwelling in modern times effects a local gradient, lowering the temperature of the higher-latitude sites along the coast by several degrees, with resultant faunal provincialism (Fig. 49). Such a mechanism could not have operated in Santonian times for two reasons. Firstly, the offshore westerly winds would have moved surface water to their left (i.e. inshore), and secondly, the north-east flowing current had its left side to the coast (and dynamic upwelling in the Southern Hemisphere occurs on the right side of currents (G. Brundrit, University of Cape Town, pers. comm. 1984)). In Table 17 the Santonian faunas from these two sites are referred to as 'cool'- and 'warm'-water assemblages (high and low latitude), respectively, but at this stage it is not clear how a significant temperature contrast between the areas was maintained. One possibility is that the boundary between them represents the southernmost limit of penetration by south-west moving inshore cells of warmer water that broke off from the regional anti-clockwise gyre to the north of the Madagascar–India landmass (Fig. 50).

On Figure 51, a temperature gradient across the north-east flowing East Coast Current is indicated, with warmer waters inshore, and cooler temperatures in the deeper and/or more oceanic areas farther offshore. This arrangement is suggested by the faunal differences between the inshore localities of Umzamba and Zululand, and the offshore localities of borehole J(c)–1 on the outer Tugela delta top and the Agulhas Bank. Although there is no substantive evidence for strong links between J(c)–1 and the Agulhas Bank until Campanian times, the presence of *Dutoitella mimica* in the Santonian of J(c)–1 suggests that the environmental conditions responsible for the faunal differences between the inshore and offshore areas around south-east Africa were already established by Santonian times. Water-temperature differences seem the most likely determinant because, although the Tugela delta top was subjected to large salinity fluctuations, there is no evidence that this was the case on the Agulhas Bank.

Recolonization of south-east Africa after the mid-Cretaceous hiatus

Dingle (1982) recognized a major dichotomy in the ostracod faunas of south-east Africa across the mid-Cretaceous hiatus, first described by Kennedy & Klinger (1971). The extent of the non-sequence varies from place to place, and at outcrop in Zululand includes uppermost Cenomanian to lower Coniacian strata

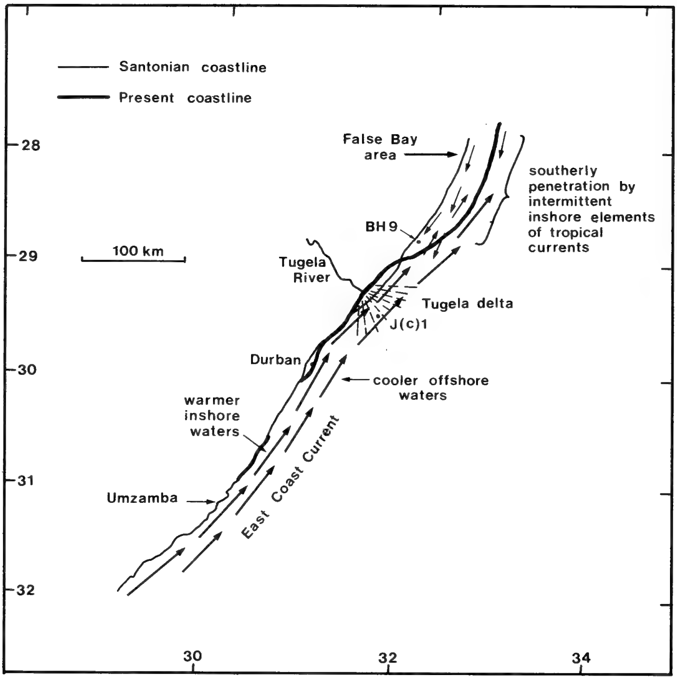


Fig. 51. Santonian palaeogeography of south-east Africa, and predicted nearshore current patterns and temperature characteristics. BH9 locates Richard Bay. Coordinates are for modern location.

(e.g. Kennedy & Klinger 1975). Boreholes closer to the coast in Zululand indicate a shorter break (?late Cenomanian to mid-Turonian—McLachlan & McMillan 1979), and suggest that the earliest sediments of the transgression become older north-eastwards (e.g. Dingle *et al.* 1983). Using Van Hinte's (1976) time-scale, the hiatus across the Mzinene–St. Lucia formations boundary varies from 3 to 6 m.y. in duration.

Figure 52 shows the temporal distribution of key ostracod taxa in south-east Africa in Valanginian to earliest Campanian strata across the hiatus. Pre-Albian assemblages are characterized by various species of genera such as *Progonocythere, Rostrocytheridea, Procytherura*, and *Acrocythere*, while Albian to Cenomanian faunas are characterized by *Arculicythere* and *Isocythereis*. These have been referred to as the South Gondwana ostracod faunas A and B, respectively (Dingle 1984). In addition, they have common elements such as *Majungaella, Sondagella, Pirileberis, Makatinella*, and *Pongolacythere* that give them added distinctiveness. With the exception of *Cythereis*, none of the cytheracean genera present prior to the mid-Cretaceous hiatus have representatives above the Cenomanian in south-east Africa, and even in this case no species are common (*C. agulhasensis*, Albian, Agulhas Bank; and *C. klingeri, C.* cf. *luzangaziensis*, and *C. mfoloziensis* in the Coniacian of Zululand). The South

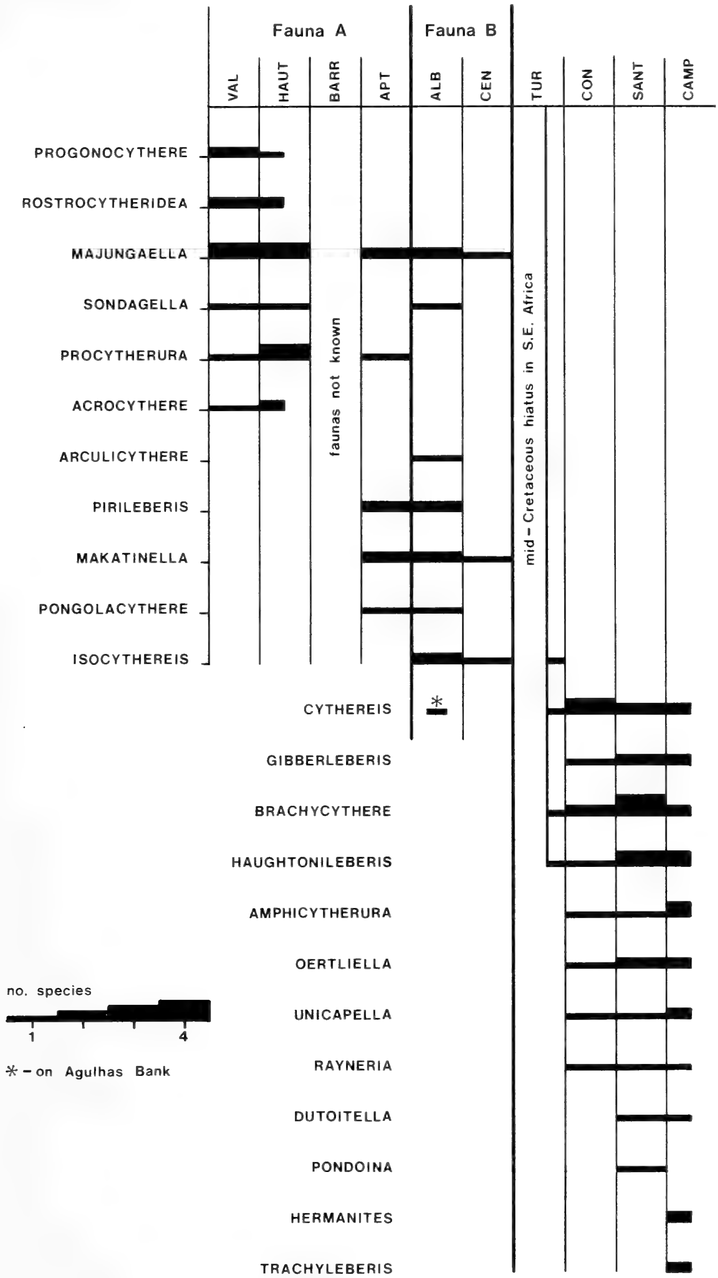


Fig. 52. Distribution of the main cytheracean genera in south-east Africa for Valanginian to Campanian time. Turonian occurrences are for Tanzania as re-interpreted from Bate & Bayliss (1969). Numbers of extant species are indicated by thickness of bars. Note the major Cenomanian–Turonian/Coniacian dichotomy. Faunas A and B are the South Gondwana faunas of Dingle (1984).

Gondwana faunas are Cytheruridae–Schizocytheridae–Progonocytheridae-dominated (Table 18).

TABLE 18

Cytheracea in south-east Africa shown as number of species (in parentheses) in families, as percentage of cytheracean element. (After Dingle 1982, 1984, this paper.)

	Haut.–Val.	Alb.–Cen.	Coniac.	Santonian
Collisarborisidae		10 (1)		
Schulerideidae		20 (2)		
Brachycytheridae			11 (1)	17 (4)
Cytheruridae	30 (6)			
Schizocytheridae	15 (3)	10 (1)	*	8 (2)
Trachyleberididae	5 (1)	30 (3)	89 (8)	46 (11)
Cytherideidae	10 (2)			4 (1)
Bythocytheridae	5 (1)	10 (1)		
Progonocytheridae	25 (5)	20 (2)		8 (2)
Loxoconchidae	5 (1)			
Indet.	5 (1)			17 (4)
Total no. spp.	(20)	(10)	(9)	(24)

* = present on Agulhas Bank

Dingle (1982) characterized post-Coniacian faunas as Trachyleberididae–Brachycytheridae–Schizocytheridae-dominated, and Table 18 and Figure 52 show that these higher taxa were all represented during Coniacian times. In other words, elements that dominated during much of Upper Cretaceous time were also aggressive recolonizers of the region after the non-sequence, in particular the long-ranging cytheracean species *Brachycythere longicaudata, Haughtonileberis haughtoni*, and *Cythereis klingeri*, medium-ranging cytheracean species such as *Gibberleberis africanus* and *Oertliella pennata*, and long-ranging non-cytheracean types such as *Bythocypris richardsbayensis* and *Cytherelloidea umzambaensis*. It is interesting to note that the earliest known member of the subfamily Unicapellinae (which forms a minor, but distinctive element of Campanian–Maastrichtian faunas) occurs in the Coniacian IV of Zululand. The total failure of the original cytheracean taxa (South Gondwana fauna B) to regain niches is a phenomenon of considerable significance, because although the sedimentary environments of Albian–Cenomanian and Coniacian–Santonian strata at Zululand outcrop sites were probably not strictly comparable, with the latter probably somewhat deeper (compare Fig. 39, this paper, and fig. 41 in Dingle 1984), the two were sufficiently similar to indicate that a combination of phylogenetic and regional palaeogeographic factors was responsible. This question will be examined in the next section.

GREATER AFRICA AND GONDWANALAND

Aspects of ostracod distribution in the South Atlantic during Cretaceous times have been considered by Krömmelbein (1976), Bertels (1977), Dingle

(1982), and Tambareau (1982*a*, 1982*b*) amongst others, and the latter references contain a comprehensive compilation of specific citations. These works have shown that the major south-east African mid-Cretaceous faunal dichotomy, which has been referred to in a previous section, is not present in west Africa and Brazil, and recent studies in north Africa (e.g. Bismuth *et al.* 1981) indicate that it is also not present along the south-west shores of Tethys. It is present in Iran (Grosdidier 1973) and Tanzania (Bate & Bayliss 1969). The problem is therefore twofold: when did the faunal change take place in south-east Africa, and why?

The difficulty in assessing the precise timing is caused by the non-sequence in uppermost Cenomanian to Turonian strata in south-east Africa, but can be tackled by considering the regional distribution of two key taxa: *Brachycythere longicaudata* and *Haughtonileberis haughtoni*. These are particularly well suited because there are numerous records of the two genera from greater Africa (Tables 6, 9); in south-east Africa the two genera, and in particular the species selected, are diagnostic elements in the post-Turonian populations (Figs 46, 48). Figure 48 shows that in Zululand *B. longicaudata* is known from Coniacian III, and *H. haughtoni* from Coniacian IV. Given the limitations of the sample distribution, both species can be considered amongst the earliest (and most abundant) colonizers of the area during the Upper Cretaceous transgression. Neither genus is present in underlying Albian–Cenomanian Mzinene Formation strata. SEM photographs of material originally described by Bate & Bayliss (1969) show that both species occur in the Upper Turonian of Tanzania (recorded as *B.* aff. *sapucariensis* and *Curfsina turonica* (paratype, BMNH Io783)). The Cenomanian–Turonian succession appears to be complete in Tanzania, but a faunal dichotomy with some of the significant characters of that noted in south-east Africa is also present here: neither *Brachycythere* nor *Haughtonileberis* occurs in the Cenomanian; and *Majungaella*, which occurs in the Albian and Lower Cenomanian, does not extend into the Turonian. In eastern Africa, therefore, the dichotomy occurs between the local top of the Lower Cenomanian (with *Rotalipora appenninica* and *Planomalina buxtorfi*), and local base of the Upper Turonian (with *Globotruncana helvetica* and *G. linneiana*, amongst others, see Table 5). In fact it could lie within the Cenomanian because Bate & Bayliss (1969: 120) record a possible intra-Cenomanian hiatus above which *Majungaella* does not occur (in beds with *Rotalipora greenhornensis* and *R. cushmani*). The latter possibility can also not be ruled out in Zululand, because the highest record so far for *Majungaella* is Cenomanian III (Dingle 1984). (No ostracod fauna was recovered from Cenomanian IV, which is probably upper *R. cushmani* Zone.) In view of the fact that Bate & Bayliss (1969) did not describe large faunas and had no ostracods of Lower–Middle Turonian age, it seems more appropriate to assume the less precise age for the faunal change at this stage of our knowledge. On the basis of ammonite faunas, Reyment & Tait (1972: 93) postulate a late Lower Turonian date at which 'nekroplanktonic ammonite shells were able to drift with oceanic currents over the entire Atlantic'. Reyment *et al.* (1976) show a series of palaeogeographies in which the various west African–Brazilian–north

African connections developed in Albian–Turonian times, and concluded that free surface-water connections between north-west Africa and the south-west Indian Ocean were established by Middle Turonian times. This accords with our data, with the exception that no trans-Saharan connection was postulated before the early Turonian (Reyment *et al.* 1976; Reyment 1980*b*). The occurrence of *Brachycythere* gr. *sapucariensis* in the Cenomanian of Tunisia, Gabon, and north-west Brazil (see Table 6) shows that at least temporary communication must have been established by early Cenomanian times, presumably across the Sahara, but conceivably around north-west Africa across the Brazil–west Africa land bridge (Fig. 53A).

Neither *B. longicaudata* nor *H. haughtoni* has been recorded from west Africa, Brazil and north Africa, but both of the genera involved have a longer history in these areas than in the western Indian Ocean region (Tables 6, 9): *Brachycythere* gr. or cf. *sapucariensis* appears in the Lower Cenomanian of Tunisia and Upper (possibly Lower) Cenomanian of Gabon, and ranges into the Lower Coniacian (Brazil), while several species of '*Haughtonileberis*' have been recorded from Gabon (Grosdidier 1979), the earliest of which is Upper Albian. In addition, four other species of *Brachycythere* occur in Lower Turonian, or older

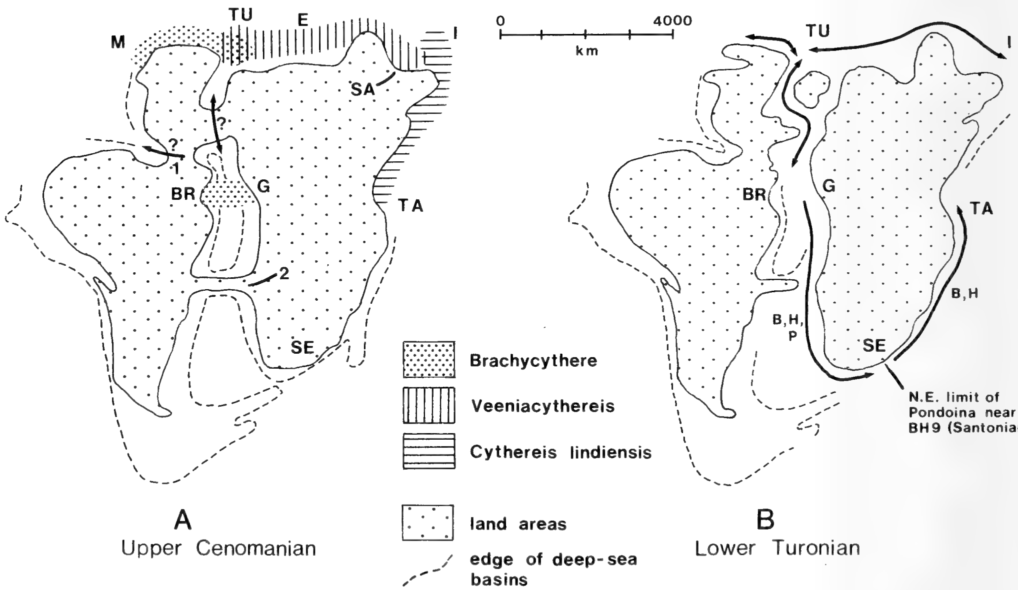


Fig. 53. Cenomanian and Turonian ostracod distributions, migrations, and intercontinental relationships. A. Upper Cenomanian. B. Lower Turonian.
Abbreviations—large type: M = Morocco, TU = Tunisia, E = Egypt, SA = Saudi Arabia, I = Iran, TA = Tanzania, SE = south-east Africa, G = Gabon, BR = Brazil; small type: B = *Brachycythere*, H = *Haughtonileberis*, P = *Pondoina*. 1 = Brazil–west Africa land bridge, 2 = Walvis–Rio Grande land bridge. Arrows denote migration routes.

strata of north Africa. *Brachycythere sapucariensis* is very close to *B. longicaudata*, and its wide geographical distribution suggests that it was probably ancestral to the latter.

From the above, it is clear that *Brachycythere* was widespread in the Equatorial Atlantic–south-west Tethys, and *Haughtonileberis* was widespread in the northern part of the South Atlantic before either genus appeared in the western Indian Ocean sometime between the Middle Cenomanian and Middle Turonian. In east Africa, they displaced the extant fauna, and in south-east Africa they colonized inshore areas during the Turonian–Coniacian transgression. Significantly, the first appearance in Iran of *Brachycythere* (five species) was in ?Coniacian–early Santonian strata (Grosdidier 1973). The questions to consider now are why did these taxa infiltrate new areas, why were they so successful, and why was there a phylogenetic 'explosion' in the newly colonized areas (many of the post-Turonian genera in south and east Africa are endemic)?

Table 6 shows that *Brachycythere* spread rapidly along the southern shores of Tethys between Morocco and Iran during Lower Cenomanian to Coniacian times. Grosdidier (1973) records a major faunal break in the latter region across a late Cenomanian to ?Coniacian–early Santonian hiatus, where the older fauna, characterized by *Cythereis* (three species), *Veeniacythereis jezzineensis*, and *Dordoniella?* is replaced by one characterized by *Brachycythere* (five species), *Veenia, Pterygocythere?, Ovocytheridea, Buntonia*, and *Cythereis*. Because *Cythereis lindiensis* is recorded in the Cenomanian of both Iran and Tanzania, indicating that there was faunal contact between the two areas in pre-Turonian times, it is superficially tempting to suggest that *Brachycythere* arrived in east Africa, and even south-east Africa, via Arabia. Other evidence does not support this suggestion, however, and in particular we can cite the restriction of *Pondoina* to Gabon (Turonian), Brazil (Coniacian), and south-east Africa (Santonian) (Krömmelbein 1972), and the non-occurrence of *Haughtonileberis* in Arabia and *Veeniacythereis* in the South Atlantic and western Indian oceans. These distributions suggest two dispersion routes out of the Equatorial Atlantic (Fig. 53B). They were favoured by different genera, so that the partitioning of the original (Cenomanian–Turonian) Gabon–Brazil fauna resulted in two generically distinct younger faunas along the southern shores of Tethys and in the western Indian Ocean.

Figure 50 shows that the region in which early evolution of *Brachycythere* and *Haughtonileberis* (Albian–early Cenomanian) took place lay in low latitudes, presumably in warm waters as part of a 'tropical' population. This suggests that water temperatures would have been a limiting factor in any migrations, at least during the early part of their development, although these genera must have been inherently more tolerant than the bulk of the Equatorial Atlantic–Tethyan tropical fauna, which never managed to achieve significant expansion into the Indian Ocean: for example *Ovocytheridea, Veenia, Veeniacythereis, Buntonia, Glenocythere*, and *Schuleridea* (see Tambareau 1982*b* for a summary). A second factor limiting migration would have been the palaeogeography of the

Equatorial–South Atlantic in Albian–Cenomanian times. Structural elevations in the vicinity of the Walvis Ridge–Rio Grande Rise and a north-west Brazil–west Africa ridge (Rand & Makesoone 1983) prevented significant communication between the two parts of the South Atlantic and the southern parts of the North Atlantic until they were modified sufficiently to allow circulation in at least surface waters. These considerations suggest that a combination of factors was necessary for the proposed migrations: partial or complete breakdown of the subaerial barriers, and the establishment of ocean currents that brought warm water into the south-east Atlantic and west Indian oceans. Both would have been dependent on the evolving palaeogeography of the fragmenting Gondwanaland. Of the two barriers mentioned, only the Walvis–Rio Grande Ridge is thought to have been significant, because the Gabon and Brazilian basins lay to the south of the north-west Brazil–west African 'land bridge', which would not have been effective in preventing trans-Saharan communication with Tunisia (Fig. 53B). The mid-Cretaceous atmospheric and oceanic circulations suggested in Figure 50 imply that once the South Atlantic had opened sufficiently, and the Walvis barrier was no longer complete, warm ocean currents, derived from the northern sector of the South Atlantic, would have provided a suitable migration route for shallow-water faunas around to south-east and east Africa. Warm water flowed into the southern South Atlantic during the winter from the anticlockwise gyre that lay to the north of the Walvis–Rio Grande Ridge. This flow may have been strengthened in the summer by currents down the west coast of Africa if the gyre reversed in a monsoon pattern (G. Brundrit, pers. comm. 1984). As a result, currents flowing down the west coast of south-west Africa were relatively warm, and would have penetrated into the palaeo- south-west Indian Ocean (Fig. 50). This model is a modification of that proposed by Neale (1976), Dingle (1982), and Tambareau (1982*b*). The fact that sedimentation had temporarily ceased in coastal south-east Africa at the height of these migrations is merely a stratigraphical complication (it was probably related to local crustal movements and/or the circulation changes that were produced by continental separation) that delayed the change in the local fossil record until sedimentation recommenced.

The success of the migrants in taking over most of the ecological niches is presumably related to the general increase in ambient water temperatures, which the incumbent (South Gondwana) faunas that had evolved in high latitudes could not tolerate. It is also suggested that the rapid phylogenetic development that occurred in Turonian–Coniacian times in the west Indian Ocean area can also be attributed to this factor. As mentioned above, only a proportion of the Equatorial Atlantic–south Tethys ostracod fauna was thermally tolerant enough to effect the migration, while the extant south-east and east African faunas were put under great stress by the arrival of new taxa and increasing water temperatures. Under the circumstances, a period of radical readjustment and speciation in occupying vacant ecological niches would be expected. Clearly, water temperatures in the west Indian Ocean, particularly as long as a north-east current flowed along the coast, would have been significantly lower than in the Equatorial Atlantic, so that

once the initial migrations had taken place, subsequent phylogenetic changes only served to differentiate the colonists from their original tropical ancestors. Consequently, south-east Africa has only a few significant faunal links with the low-latitude Atlantic areas, but relatively strong links with east Africa, whose faunas developed under similar circumstances.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .': '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
(c) Scientific names, but not their vernacular derivatives
e.g.Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

R. V. DINGLE

TURONIAN, CONIACIAN, AND SANTONIAN OSTRACODA FROM SOUTH-EAST AFRICA